FACTEURS MOTIVANT LE CHANGEMENT DE TÉTINES CHEZ LE VEAU (*Bos taurus*)

par

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L'allaitement est important pour la croissance et la santé des jeunes mammifères. En plus de la tétée, les veaux font des changements de tétine, donnent des coups de tête au pis, glissent la bouche sur la tétine et relâchent les tétines. On croit que le changement de tétine survient lorsque le veau perçoit une réduction du débit de lait du pis au moment où une des quatre citernes se vide. Cependant, puisque le débit de lait du pis n'a jamais été mesuré pendant la tétée, nous ne pouvons savoir avec certitude si ces comportements sont effectivement causés par des réductions dans le débit de lait. Dans la présente étude, j'ai utilisé un appareil d'alimentation ayant deux tétines, permettant de contrôler le débit de lait avec précision et ce, dans le but de vérifier plusieurs hypothèses. Dans un premier temps, j'ai pu vérifier au moment du repas qu'un débit de lait constant, mais réduit, amenait le veau à changer plus souvent de tétine et à augmenter le nombre de coups de tête. En effet, une soudaine réduction du débit de lait était suivie de coups de tête et d'un changement de tétine. J'ai observé la tendance des changements de tétine durant les premières 2,5 minutes d'un repas à un constant débit *de base*, (soit 0,66 l/min). Suivant une période initiale de 30 secondes où les veaux changeaient de tétine très fréquemment (6 changements/min), j'ai calculé une fréquence moyenne d'un changement par min (1 changement/min), et ce, dans le traitement où les veaux avaient accès à deux tétines nutritives ainsi que lorsqu'ils avaient le choix entre une tétine nutritive et une tétine non-nutritive. Il n'y avait pas de différences significatives dans la fréquence des coups de tête d'un intervalle à l'autre tout au cours de la période d'observation et la moyenne variait de 2 à 2,5 coups/min, indépendamment du nombre de tétines nutritives disponibles. La fréquence des relâchements de tétine et des glissements de la bouche était également relativement constante durant les premières 2,5 minutes du repas. Par ailleurs, si l'on fait la somme des coups de tête, des relâchements de tétine et des glissements de bouche (i.e. les *comportements dirigés vers la tétine*), leur fréquence collective était deux fois plus

élevée au cours des premières 30 secondes du repas que durant le reste de la période d'observation. Il a également été observé que le débit de lait avait un impact sur les comportements. En effet, lorsque le débit des deux tétines étaient *extrêmement lent* (0,04 l/min), une augmentation des fréquences de chacun des comportements a été observée soit, les changements de tétine, les coups de tête et les glissements de bouche et ce par un facteur de 4, 2 et 3 respectivement. De même, la fréquence des relâchements de tétine est passée de 0 à 1 relâchement/min, en comparaison au débit *de base*. Il y a eu trois changements de tétine de plus lors des 30 premières secondes du repas comparativement aux 30 secondes suivantes. Les *comportements dirigés vers la tétine* étaient également plus fréquents lors de la première période (11 vs. 8 comportements dirigés par minute au débit *extrêmement lent* et 6 vs. 3 comportements dirigés par minute au débit *de base*). Lorsqu'une tétine présentait un débit *extrêmement lent* et l'autre un débit *de base*, les veaux restaient 95% du temps de la période d'observation sur la tétine au débit *de base*, et leurs comportements étaient alors identiques à ceux observés lors de l'expérience où les deux tétines livraient le lait au débit *de base*. De plus, les veaux démontraient une préférence marquée à l'intérieur d'un repas, pour une des deux tétines, y passant 83% du temps et seulement 17% du temps sur l'autre lorsqu'elles présentaient tous deux un débit *de base.* Lorsque les tétines étaient au débit *extrêmement lent* les veaux passaient 60% du temps du repas sur une tétine mais seulement 40% du temps sur l'autre. Le choix d'une ou l'autre des tétines n'était, par contre, pas constant d'une expérience à l'autre. Afin de tester l'hypothèse qu'une réduction du débit de lait entraîne un changement de tétine, le débit de lait était soudainement réduit du débit *de base* à un débit *extrêmement lent* ou à nul. Lorsque les veaux étaient exposés à ces réductions de débit, ils changeaient de tétine 8 à 9 fois plus fréquemment que lorsque le débit était maintenu constant, au débit *de base*. De plus, la fréquence des changements de tétine était proportionnelle à l'ampleur de la réduction de débit. Par ailleurs, ce comportement ne semblait pas être affecté quand la seconde tétine ne livrait pas de lait. Les veaux changeaient de tétine 1 fois sur 5 lorsque le débit était réduit au débit *lent* (0,46 l/min), et 4 fois sur 5 lorsque le débit était arrêté. La tendance des comportements de coups de tête semblait similaire: comparativement au débit *de base*, ceux-ci n'augmentaient pas lorsque le débit était réduit au débit *lent*, alors qu'ils étaient 5 fois plus

fréquents lorsque le débit était arrêté. En conclusion, ces expériences m'ont permis de faire les constats suivants: (a) les comportements de changements de tétine, de coups de tête et l'ensemble des *comportements dirigés vers la tétine* sont de façon générale plus fréquents au cours des premières 30 secondes d'un repas, et ce malgré un débit de lait constant; et leur fréquence diminue ensuite sans toutefois disparaître complètement; (b) à un plus faible débit j'observe la même tendance mais la fréquence de chaque comportement augmente; et (c) lorsque le débit de lait est soudainement réduit, les veaux donnent des coups de tête suivis par un changement de tétine et ces réponses sont proportionnelle à l'ampleur de la réduction de débit. Mes résultats semblent donc indiquer que les veaux ont la capacité de détecter une réduction de débit de lait et que ce dernier leur stimule à faire des changements de tétine et des coups de tête. Les comportements de coups de tête et de changements de tétines sont peut-être utilisés durant l'allaitement du jeune sur la mère pour stimuler l'éjection du lait de la glande mammaire. Une deuxième raison pouvant potentiellement expliquer le changement de tétine, serait la motivation du veau de retrouver une tétine livrant un débit de lait plus rapide. Reconnaître la motivation des changements de tétine et des coups de tête chez le veau pourrait être utile pour détecter les problèmes potentiels de faible débit de lait chez la vache allaitante ainsi que provenant des appareils d'alimentation. Par contre, il est important de ne pas interpréter les changements de tétine frénétiques, en début de repas, comme l'indication d'un faible débit. Il semble que ces comportements sont bénéfiques et seraient le résultat de la sélection naturelle. Ces résultats pourraient ainsi être utilisés en tant qu'indicateur du débit de lait chez les femelles allaitantes d'autres groupes d'ongulés, étant donné leur proximité phylogénétique aux bovins domestiques.

ABSTRACT

FACTORS THAT MOTIVATE TEAT-SWITCHING IN THE CALF (*Bos taurus*)

Nursing behaviour in young mammals is very important for growth and to maintain health. In addition to sucking behaviour, dairy calves teat-switch, butt at the udder, teat-strip and release the teats. It has been suggested that teat-switching occurs when there is a decrease in milk-flow rate from the udder, which is thought to occur when a calf empties one of the four udder cisternae. However, since changes in milk-flow rate from the udder have never been measured during nursing, it is not known whether milk-flow rate affects teat-switching behaviour. Using a feeding apparatus equipped with 2 teats which allowed the precise control of milk-flow rate, I tested various hypotheses. Firstly, that calves would teat-switch and butt more frequently when the flow rate of milk was constant, but reduced, and that a sudden reduction in flow rate would result in butting and then a teat-switch. I first studied the pattern of teat-switching during the first 2.5 minutes of the meal at a constant *baseline* flow rate (0.66 l/min). When calves had 1 nutritive and 1 non-nutritive teat; or 2 nutritive teats, they did about 1 teat-switch/min except in the first 30 seconds of the meal when they did 6 switches/min. Butting rate was 2 - 2.5 butts/min when they had either 1 nutritive teat; 1 nutritive and 1 non-nutritive teat; or 2 nutritive teats. Butting, stripping and teat-releasing did not vary from interval to interval throughout the observation period but the collective frequency of these 3 behaviours (*teat-directed behaviours*) in the first 30 seconds was double that during the rest of the observation. Milk-flow rate had an effect on each component of behaviour. When milk-flow rate from both teats was *extremely-slow* (0.04 l/min), calves teat-switched 4 times as often; butted twice as often; stripped 3 times as often and increased their teat-releasing from 0 to 1 release/min compared to the *baseline* flow rate. In the first 30 seconds of the meal, calves did 3 more switches than in each of the next 30-second intervals, both at the *extremely-slow* and at the *baseline* flow rates although overall switching was consistently higher when both teats were *extremely-slow*. Teat-directed behaviours also occurred more frequently in the first 30 seconds of the meal: 11 vs. 8 teat-directed behaviours per min at *extremely-slow* and 6 vs. 3 teat-directed behaviours per min at *baseline*. When one teat was at *baseline* and the other was *extremely-slow*, calves spent 95% of their time on the *baseline* teat and thus their behaviour in

this test did not differ from when both teats were at *baseline*. Within a meal, calves showed a strong preference for one teat, spending 83% of their time on one versus 17% on the other when both teats were at *baseline* and 60% of their time on one and 40% on the other when both teats were of the *extremely-slow* flow rate. The teat chosen was not consistent across experiments for a given calf. Finally, to test the hypothesis that a sudden decrease in milk-flow rate would result in a teat-switch, milk-flow rate was reduced from *baseline* to *extremely-slow* or to nil. Following the reduction in milk-flow rate, calves switched 8 - 9 times more often and butted twice as frequently as when milk-flow rate was not changed. The probability of switching was proportional to the magnitude of the reduction. The availability of a non-nutritive, second teat did not affect the teat-switching nor the butting response of calves. Calves did not switch when milk-flow rate was not reduced, they switched 1 out of 5 times when the flow rate was reduced to *slow* (0.46 l/min) and 4 out of 5 times when the flow was turned off. Butting followed a similar pattern: when milk-flow rate was reduced from *baseline* to *slow*, calves did not butt more than when milk-flow rate was not reduced but butting increased 5-fold when milk flow was turned off. I conclude that teat-switching, butting and *teat-directed behaviours* are much more frequent in the first 30 seconds of the meal despite a constant flow rate. These behaviours decrease in frequency as the meal progresses but do not disappear completely. At a reduced flow rate, the same pattern emerges but the overall frequency of all behaviours is increased. My results suggest that calves are sensitive to changes in milk-flow rate and that they respond to a sudden decrease in flow rate by butting and then switching teats, generally in proportion with the magnitude of the reduction. Teat-switching and butting are useful behaviours for inferring possible flow-rate problems in calves on the dam or calves nursing from an artificial teat. It is important, however not to interpret the initial, frenetic teat-switching as resulting from a reduced milk-flow rate. Instead, these behaviours are likely used by the calf to increase its milk intake by stimulating milk flow from the cow or by leading the calf to a more productive teat and appear to be the result of natural selection. These results could also be applicable to other ungulates as an indicator of milk-flow rate, given their phylogenetic relationship to domestic cattle.

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CHAPTER 1
INTRODUCTION

1.1 General introduction

Nursing is an important behaviour for survival and it is one of the defining characteristics of the mammalian class. Young animals suck milk from their mother's mammary glands because it is important for nourishment and required for health, growth and ultimately reproductive success (Festa-Bianchet, 1988). Consequently, it would be expected that sucking behaviour would change as resource availability increased or decreased.

While sucking, animals perform other teat-directed behaviours which are thought to be stimulatory, since manipulation of the skin of the mammary glands results in a physiological process that leads to milk ejection (Gorewit and Gassman, 1985). Because ungulate juveniles typically nurse while standing, the only parts of their bodies available to stimulate the udder are the head and mouth. During a nursing, it is common to see young ungulates use their heads to vigorously butt at their mother's udder (Lent, 1974). In cattle, butting occurs mostly at the beginning of a nursing bout and just before the calf switches to another teat (Horrel, 1993; Lidfors *et al.*, 1994).

Many studies have investigated nursing behaviour in calves, but most have concentrated on the total duration and frequency of bouts, while few have examined why calves perform the other behaviours that occur during a nursing, such as teat-switching. The goal of my research was to examine the effect of milk-flow rate on teat-switching behaviour and to study the patterning of teat-switching at the beginning of the meal. I also looked at other teat-directed behaviours such as butting, teat-stripping and teat-releasing to gain an overall understanding of the behaviours associated with nursing.

Calves butt at higher frequencies just before switching to another teat, so it has been presumed that the calf has drained the udder-quarter from which it is sucking, causing milk-flow rate to decrease which motivates butting and then a teat-switch (Lidfors *et al.*, 1994; Mayntz *et al.*, 1996). Since cows have four teats and each one drains a separate mammary gland within the

udder, when one quarter is emptied, the others are not affected. Therefore, by switching to another teat, the calf arrives at a full cistern of milk.

De Passillé *et al.* (1996) showed that reducing the quantity of milk in a cow's udder by milking it before a nursing resulted in an increase in butting behaviour in calves. Haley *et al.* (1998a) devised feeding apparatus which allowed calves to suck for their meal at precisely controlled milk-flow rates and demonstrated that indeed a slow milk-flow rate or a stoppage in milk-flow resulted in increased butting. The question of whether a reduced milk-flow rate motivates a teat-switch has never been studied. I therefore set out to test the hypothesis that following a sudden reduction in milk-flow rate, calves would switch teats to maximise milk intake and possibly to stimulate the dam.

In order to determine that its current rate of food acquisition is low, an animal must have some way of evaluating the quality of its feeding patch. An animal uses its prior knowledge as well as the sampling information it gains through foraging to gain knowledge of its environment (Valone and Giraldeau, 1993). To assess whether the milk-flow rate from a teat is adequate calves could compare it to flow rates during previous nursings, as well as from sampling the immediate milk-delivery rate from other teats, during a nursing.

At the beginning of the meal, calves frenetically butt and teat-switch and continue to perform these behaviours throughout the meal, but at a much lower frequency (Horrel, 1993; Lidfors *et al.*, 1994). It has been supposed that the initial butting and teat-switching at the start occur because milk-flow rate is slow before milk ejection (Mayntz, 1995; 1996). However, these behaviours are also observed in calves sucking on dairy cows which are known to have a high quantity of milk in their cisternae (Sagi *et al.*, 1980) and thus milk which is immediately available. In addition, Haley *et al.* (1998a) observed that calves butted more frequently during the first minute of the meal than in the "middle minute" of the meal. These results were obtained by observing calves drinking from a feeding apparatus which had a steady milk flow right from the beginning of the meal. Therefore a reduced milk-flow rate is not the only motivator for butting and I suspect that it is not the only motivator for teat-switching either. I was interested in testing whether teat-switching followed the same pattern as butting at the beginning of the meal such that calves would frequently teat-switch in the first minute of the

meal and that this behaviour would continue to occur, but much less frequently in the following minutes despite a constant milk-flow rate.

Teat-switching could serve two functions, both to stimulate the udder and also to provide information to the calf about the flow rate in the other teats. Since it is not possible to eliminate either of these functions, I have reviewed the relevant literature on both topics. Both functions would generate the same predictions, because calves would be expected to teat-switch at a high frequency at the beginning of the meal to stimulate the milk-ejection reflex and they would be expected to do so to acquire information on the flow status of the other teats, then nurse at the teat delivering milk at the fastest rate. Following this high activity, calves would be expected to perform a lower level of teat-switching to maintain stimulation of the dam or to continue monitoring the other teats for any changes in milk flow. This reasoning also predicts that at a slower but constant milk-flow rate, calves would show an overall increase in teat-switching but in the same general pattern described above.

A better understanding of the motivation for teat-switching and teat-directed behaviours could provide information about milk quantity and flow rate within the udder during a nursing, without the use of invasive techniques. The information could be used by producers as an indicator of an insufficient milk-flow rate from a dam or from a feeding apparatus which would allow him/her to investigate the situation and rectify the problem before suffering economic losses. These results could also be applicable to other ungulates, given their phylogenetic relationship to domestic cattle.

1.2 The bovine udder

In cows, milk is synthesised in the alveolar cells of each of four mammary glands which are collectively called the udder. The cells form the walls of small blind sacs called alveoli (Figure 1a). When newly synthesised milk exits the cells, it collects in the alveoli. Below each gland is a cistern which extends into the teat and acts as a receptacle to hold milk that descends from the alveoli. The teats are about 6 cm long, 3 cm in diameter and have a single opening at their tip which ranges from 4-11 mm in length (Figure 1b).

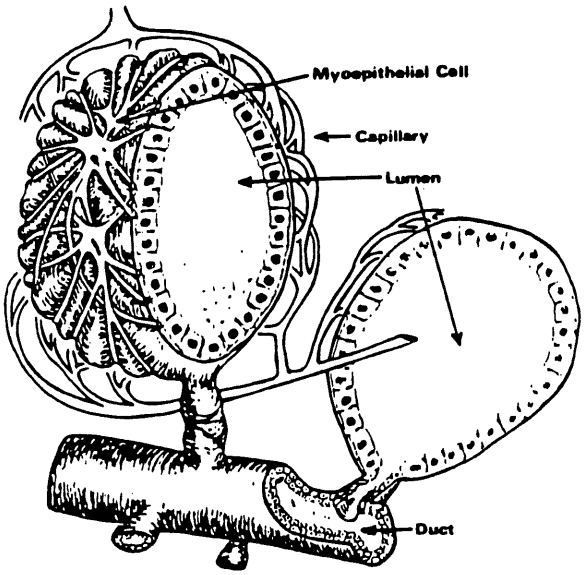

Figure1a. Diagram of an alveolus surrounded by myoepithelial cells (Larson, 1985)

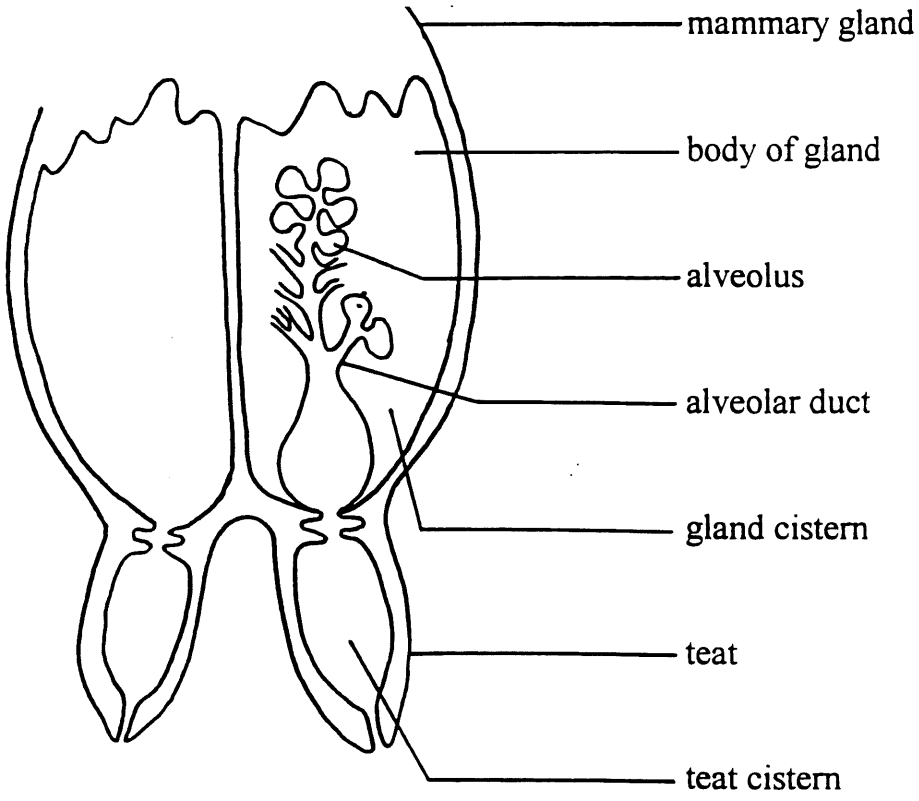

Figure 1b. Diagram of the cross-section of a mammary gland

1.3 The milk-ejection reflex

Milk normally descends from the alveoli into the cisternae but during a nursing milk is forced out of the alveoli via the milk-ejection reflex. This physiological process increases the pressure within the udder and causes the milk to be ejected at increased flow rates (Gorewit *et al.*, 1983; Gorewit and Gassman, 1985). The skin of the teats and udder are innervated with pressure-sensitive receptors. Stimulation of these regions for 30 seconds results in the release of a hormone called oxytocin from the pituitary gland (Gorewit and Gassman, 1985). The hormone is then transported via the circulatory system to receptors on myoepithelial cells which surround the alveoli and the alveolar ducts. Oxytocin causes these cells to contract, which squeezes alveolar milk into the cisternae (Cross, 1954; 1961; Lefcourt and Akers, 1966; Sagi *et al.*, 1980; Gorewit *et al.*, 1983; Mayer *et al.*, 1984).

The release of oxytocin takes about 30 to 60 seconds (Cross, 1961) and corresponds to the period, during a nursing, when calves excitedly teat-switch and perform other teat-directed behaviours (Horrel, 1993; Lidfors *et al.*, 1994). Teat-switching at the beginning of the meal increases the surface of skin that calves touch and thus stimulate. Since sensory stimuli are additive (Shepherd, 1988), touching the skin of two teats may cause a greater milk ejection than simply stimulating one teat.

Milk secretion is independent of motor innervation (Cross *et al.*, 1958; Findlay, 1968; Findlay and Grosvenor, 1969). There are few nerves that reach the interior of the udder and those associated with the exterior gland innervate the smooth muscle responsible for the udder's tautness. When these nerves are stimulated, the gland and teats contract and milk flow is inhibited (Shmidt, 1971).

1.4 Calf rearing

Beef calves are usually raised in free range conditions and allowed to nurse the dam until weaning, which occurs at 7 to 10 months, depending on the breed (Le Neindre and Petit, 1975; Reinhardt and Reinhardt, 1981). By contrast, male dairy calves are usually raised for veal production and slaughtered at 20 weeks and females are raised as replacement dairy cows. Calves of both sexes are usually removed from their mother at or soon after birth and fed milk

replacer so that their mother's milk may be harvested and sold for human consumption (Edwards and Broom, 1982).

1.5 The basic biology of nursing

1.5.1 The first nursing

Calves have an innate drive to nurse. Within the first hour post-partum, a calf makes its first attempt to stand and search for one of its mother's teats. The search is directed at the inguinal region of the dam, and the calf will suck any object resembling a teat, like the mother's tail, for example (Selman *et al.*, 1970; Edwards, 1982; Lidfors and Jensen, 1988). In artificial calf rearing, only 70 to 83% of calves are able to stand up and nurse within six hours post-partum (Selman *et al.*, 1970; Edwards, 1982; 1983). Factors that delay the time until the first suckling include poor maternal behaviour such as calf rejection, a pendulous udder conformation and low calf-vigour. However, once a calf has nursed, it no longer has trouble locating a teat (Walker, 1950; Selman *et al.*, 1970; Edwards and Broom, 1982).

During the first four days post-partum, the calf drinks the antibody-rich colostrum that the mother produces. This substance confers passive immunity to the calf (Edwards and Broom, 1982) but as the calf ages, its ability to absorb these antibodies decreases (Stott *et al.*, 1979; Edwards, 1982) so a strong nursing drive is particularly important in the initial days of life.

1.5.2 The anatomy of a nursing bout

Lidfors *et al.* (1994) were among the first to describe in detail the behavioural patterning of a nursing episode in beef cattle. Two types of sucking were defined: "nutritive sucking" which was characterised by 2.1 sucks/second done in a rhythmic manner and interpreted as being the main period of milk intake, and "non-nutritive sucking" which was distinguished by frequent butts at the udder and teat-releases. The authors called this phase "non-nutritive" because they speculated that during the period with butts and teat releases the calves were probably obtaining little or no milk. Much teat-switching and butting behaviour was observed during the first minute of the nursing followed by calmer, rhythmic, nutritive sucking for 4 to 5 minutes.

Butting occurred throughout the nursing but increased near the end just before the calf switched to another teat.

Similarly, Mayntz *et al.* (1995, 1996) described four different periods of a sucking episode on a given teat. The first period lasted about 81 seconds and consisted of short bouts of uninterrupted sucking at the beginning for pre-stimulation. The next relatively short period (about 110 sec in length) was termed full-ejection since at this point the cisternae rapidly filled with milk. During this period, the duration of sucking bouts were maximised. Next was declining ejection followed (lasting 162 seconds, on average), where calves were able to drink the milk faster than it became available which resulted in shorter sucking-bout lengths. Lastly, at the end of milk ejection, during the period when milk was very scarce (lasting about 242 sec), sucking bouts were very short and this period was termed after-stimulation. Mayntz *et al.* (1995, 1996) claimed that calves had the motivation to remain on one teat until all four stages of the sucking bout were completed. He did not specify what the calf did between sucking bouts, but presumably they were teat-switching, butting or simply releasing the teat.

At the end of a nursing when the calf has sucked at all four teats, it alternates quickly from one teat to another, briefly taking each teat in its mouth (Hammel *et al.*, 1988; Mayntz, *et al.* 1996). At this point, the calf has presumably drained all four teats, so that each time it tries a new one, the new one is empty or has only begun to fill as milk is synthesised. As a result milk-flow rate is reduced.

1.5.3 Frequency and duration of nursing bouts

New-born calves suckle up to four times within the first eight hours of birth and an individual nursing can last up to 15 minutes (Selman *et al.*, 1970; Lidfors and Jensen, 1988). The most common dam-calf position during the first nursings is the reverse parallel, where the calf is sucking at the mother's udder, and the dam is licking the calf's ano-genital region. As calves get older, they can nurse in many different positions, including sucking a teat from between the dam's hind legs (de Wilt, 1985).

At one month of age, calves nurse about 4-5 times in a 24 hour period (Table 1). Nursing rate declines as calves age so that by 6 months they are nursing half as frequently. The duration of

Table 1. Frequency and duration of nursing bouts of beef calves on their dams

Ave calf age (days)	Frequency (bouts/24 hrs)	Duration of bout (minutes/24hrs)	Author(s)
1 (1st nursing)	-	13.2	Lidfors and Jensen, 1988
1	7.5	10	Fraser and Broom, 1990
1	7.4	8.6	Lidfors, 1994
1	-	14	Lidfors and Jensen, 1988
3	6.2	9.1	Lidfors, 1994
3.5	14	8	Spinka and Illman, 1992
7	-	12	Lidfors and Jensen, 1988
23	5.5	8.9	Hafez and Lineweaver, 1968
15	4[1]	8.5[1]	Nicol and Sharafeldin,1975
30	3[2]	10[2]	Ewbank, 1969
30	4.6	8.4	Drewry *et al.*, 1959
30	5.5	6.9	Sommerville and Lowman, 1979
30	8	8	Reinhardt and Reinhardt, 1981
45	5.5	10.7	Sommerville and Lowman, 1979
45	8.6	7.8	Day *et al.*, 1987
45	6[1]	-	Le Neindre and Petit, 1975
60	2.5[2]	8[2]	Ewbank, 1969
60	-	12	Lidfors and Jensen, 1988
90	2.3[2]	7.4[2]	Ewbank, 1969
90	4.8	11.6	Drewry *et al.*, 1959
90	6.5	8	Reinhardt and Reinhardt, 1981
105	5.9	8.6	Day *et al.*, 1987
105	4.5[1]	9.5[1]	Petit, 1972
120	-	10	Lidfors and Jensen, 1988
165	4.5	9.8	Day *et al.*, 1987
180	4.5	-	Fraser and Broom, 1990
180	4	8	Reinhardt and Reinhardt, 1981
180	3	10.2	Drewry *et al.*, 1959
195	4[1]	-	Le Neindre and Petit, 1975
210	2.5[1]	15[1]	Petit, 1972
0 to 90	4.9	10.4	Lewandrowski and Hurnik, 1983
1 to 120	5	9.2	Odde *et al.*, 1985
0 to 180	4.3	9.9	Lidfors and Jensen, 1988
10 to 180	8	9.9	Shimada *et al.*, 1989
30 to 90	-	8.7	Mayntz *et al.*, 1996
30 to 120	5	9.2	Odde *et al.*, 1985
0 to 210	4	9	Walker, 1950; 1962
1 to 225	4.7	10.4	Wagnon, 1963

1) "dusk to dawn"; 2) period of observation: 12 hours

each bout remains relatively constant at 8-10 minutes from 2 weeks onward. There is some disagreement as to whether there are differences between the sexes in nursing patterns. Males have been observed to suckle and stimulate their dams more frequently than their female counterparts (Melton *et al.*, 1967) but some authors have found no sex-differences in frequency, duration or total time spent nursing (Le Neindre and Petit, 1975; Lidfors and Jensen, 1988).

Nursing bouts are mainly concentrated at dawn and at dusk with very few episodes during the night (Hafez and Lineweaver, 1968; Le Neindre and Petit, 1975; Reinhardt and Reinhardt, 1981; Odde *et al.*, 1985; Day *et al.*, 1987), and over 80% of nursing bouts are both initiated and terminated by calves (Wagnon, 1963; Lidfors *et al.*, 1994).

1.5.4 Milk intake by calves

The frequency and duration of nursing bouts is not necessarily an accurate indication of how much milk has been drunk (Festa-Bianchet, 1988; Babbitt and Packard, 1990; Lidfors et al., 1994; Cameron, 1998). Such variables as milk production and thus milk-flow rate, calf hunger and sucking vigour determine the rate of milk intake (Mendl and Paul, 1998). It was observed that higher-producing cows were sucked less frequently than lower-producing ones presumably because calves were getting ample milk from the former, but in less visits (Le Neindre and Petit, 1975; Day *et al.*, 1987). Another difficulty in determining the quantity of milk obtained by a young mammal is that within a nursing there are periods of non-nutritive sucking, where no milk is obtained (Lidfors *et al.*, 1994).

De Passillé *et al.* (1996) showed experimentally that when cows were totally milked a half hour before a nursing (thus reducing the quantity of milk in the udder and presumably milk-flow rate), calves spent twice as long sucking for their milk than when the dam had only been partially milked, although both groups drank the same quantity of milk. Over the longer term, Lidfors and Jensen (1988) found no correlation between calf weight at weaning and overall sucking duration and frequency, however Odde *et al.* (1985) reported that heavier calves sucked their dams less frequently than lighter ones.

During a normal nursing bout, younger calves consume about 5-6 kg of milk. The amount of milk consumed increases to about 10 or 11 kg when calves are older, (Table 2) but there is much variability among different breeds and presumably among individuals within a breed.

Table 2. Quantity of milk consumed by different breeds of beef calves

Breed	Age of calves (weeks)	Quantity of milk drunk (kg/day)	Author(s)
Polish Black & White	1 to 10 days	8.6	Metz, 1987
Angus crossbred	1	8.6	Dove and Axelson, 1979
Angus	1	6.3	Dove and Axelson, 1979
Angus crossbred	1	5.2	Mezzadra *et al.*, 1989
Charolais crossbred	1	6	Mezzadra *et al.*, 1989
Nelore crossbred	1	8	Mezzadra *et al.*, 1989
Angus crossbred	1.5	11.2	Dove and Axelson, 1979
Angus	1.5	10	Dove and Axelson, 1979
Angus crossbred	1.5	6.9	Mezzadra *et al.*, 1989
Charolais crossbred	1.5	8.2	Mezzadra *et al.*, 1989
Nelore crossbred	1.5	8.5	Mezzadra *et al.*, 1989
Japanese Black	1.5	4.4	Shimada *et al.*, 1989
Japanese Polled	1.5	5.9	Shimada *et al.*, 1989
Salers	7.5	9.3	Le Neindre and Petit, 1975
Limousin	7.5	5.7	Le Neindre and Petit, 1975
Charolais	7.5	5.8	Le Neindre and Petit, 1975
Aubrac	7.5	5.9	Le Neindre and Petit, 1975
"Tachetée de l'est"	7.5	6.6	Le Neindre and Petit, 1975
Japanese Black	25	2.6	Shimada *et al.*, 1989
Japanese Polled	25	3.5	Shimada *et al.*, 1989

Calf hunger can also affect the duration of a nursing and the quantity of milk consumed. Calves that had only drunk 50% of their regular meal-quantity of milk at the previous meal sucked for longer and drank more at the following meal than those whose previous meal had not been reduced. Similarly, calves that had 4 l of milk delivered directly into their stomachs 10 minutes prior to the test were physically satiated and thus nursed their mother for less time and consumed less milk (de Passillé *et al.*, 1996).

Therefore, based on the evidence, it is unwise to use nursing time to measure milk transfer (Cameron, 1998). However, since it has been shown that butting results when milk-flow rate is reduced (Haley *et al.*, 1998a) this behaviour could be used as an indicator that milk transfer is slow. Teat-switching may also prove to be an indicator of a slow milk flow and thus of a slow milk transfer.

1.5.5 Non-nutritive sucking and natural nursing

During a nursing, there are moments when there is no milk transfer even though the calf is sucking on a teat. This behaviour has been termed non-nutritive sucking and it is a normal part of nursing that occurs in many species of mammals (de Passillé and Rushen, 1997; Cameron, 1998). In addition, young animals sometimes suck on their mother's teats between nursings, when there has not been sufficient time for new milk to be produced. One explanation for sucking without milk reward is that non-nutritive sucking is thought to have a pacifying effect (Lent, 1974), since animals and infants show this behaviour when they are distressed or frightened (Wolfe, 1968). This behaviour has also been suggested to be important in reinforcing the mother-young bond (Festa-Bianchet, 1988).

At the termination of a nursing bout, when butting and teat-switching are frequent, calves persist in sucking even though it has been suggested that they are probably receiving little or no milk (Lidfors *et al.*, 1994). However, the sucking at the end of the bout is important because it ensures that the udder is properly emptied (Mayntz *et al.*, 1996). In the short term, draining the udder acts to maintain milk production at a maximum, since residual milk in the udder has an inhibitory effect on further milk production because it contains a specific protein molecule called FIL (feedback inhibitor of lactation) (Wilde and Peaker, 1990; Wilde *et al.*, 1995). In the long term, complete draining of the udder causes mammary cells to increase their secretory activity (Svennersten *et al.*, 1990). Therefore, for optimal milk production, all four cisternae should be completely emptied regularly (Akers and Lefcourt, 1984).

1.6 Domestication and ethology

Although domestic animals have been selectively bred to enhance characteristics important to humans, including behavioural traits, they remain suitable models for studying problems in

animal behaviour. Within certain limits, results from domestic animals can be extrapolated to wild species. Traits in domestic animals which have not been artificially selected for, such as a high motivation to suck, butt and teat-switch have most likely been carried down from their ancestors. Although it can not be known for certain which characteristics are ancestral, it is highly improbable that behaviours which would be adaptive in the wild would arise just by chance, after domestication, independently of natural selection (Price, 1984), especially when these behaviours can still be observed in the wild in related species.

In addition, the selective regimes that likely led to the evolution of many behaviours are usually not present in an animal's modern environment, supporting the idea that the behaviours could not have evolved in such an environment. However, since nursing efficiency would have been so important in the ancestral environment, every surviving individual would have possessed the trait and passed it on. This set of behaviours may have disappeared in the modern population, in the absence of natural-selective pressure, if they had been maladaptive or if animals devoid of these characteristics were artificially selected for. However, the retention of nursing-associated and many natural behaviours have been demonstrated by observing farm animals kept in their natural environments (Price, 1984; Rushen, 1995). In fact, although nursing efficiency is not a trait which is specifically selected for in modern husbandry, inefficient suckling would result in poor weight gain and thus, these calves would not be chosen to sire offspring.

1.7 Foraging theory and its relevance to nursing behaviour in calves

The principle of natural selection is the paradigm on which evolutionary theory is based. According to this theory, animals are selected to behave in manners which maximise their fitness. Since it is often difficult to measure fitness, which is defined as an animal's relative contribution to the genetic make-up of the subsequent generation, currencies which are thought to correlate well with fitness are chosen as measures. An example of a currency often measured in the foraging literature is *rate of energy intake* (Maynard Smith, 1978) under the assumption that, for an animal to maximise its fitness, it must maximise its energy intake. According to theory, optimal behavioural decisions are those which maximise benefits and minimise costs based on the immediate environmental constraints (Goodenough, 1993; Krebs and Davies, 1993). To illustrate this principle using the currency described above, when an

animal is foraging in a food-patch, it is faced with the decision of when it should leave to go to a new food-patch. The potential benefit of leaving is that it may find a more profitable food-patch elsewhere, but the associated cost is the energy it expends to travel and search instead of feeding. To maximise fitness, animals may have to behave less optimally in the short run in order to behave optimally and exploit the richest areas over the long run (Smith and Sweatman, 1974; Pyke *et al.*, 1977; Krebs *et al.*, 1978; Maynard Smith, 1978; Tamm, 1987; Shettleworth *et al.*, 1988). The decision of when to leave a patch is based on prior information as well as information the animal acquires by sampling other sites while foraging (Valone and Giraldeau, 1993). Different models suggest different rules that animals may follow in making the decision to move on or to stay in a patch (Charnov, 1976; McNair, 1982).

Time is a constraint in foraging, this is particularly true when the source of nourishment can actively displace itself or is ephemeral. When young animals nurse, it seems reasonable to presume that energy intake is most likely maximised and presumably in the least amount of time possible, since the mother can potentially move away from the sucking young.

1.7.1 Sampling feeding sites

Sampling allows animals to compare the quality of the patch being exploited to the estimated quality of the other patches within the environment. The theory is therefore based upon the assumption that animals are able to assess patch quality and have some knowledge of the average patch quality (Krebs *et al.*, 1978; Valone and Giraldeau, 1993; Krebs and Davies, 1997). Teat-switching may function to provide calves with information about the flow rates of the various mammary glands of the udder.

Different animals may use different strategies, and individual animals may use a combination of different rules based on the current environmental situation, but little is known about how much time animals should invest to acquire information about the environment (Pyke *et al.*, 1977; Krebs *et al.*, 1978; Tamm, 1987). It has generally been observed that animals increase their sampling time as the quality of the patch they are exploiting decreases (Kramer and Weary, 1991).

Because I expected calves to monitor their environment by sampling, I hypothesised that they would occasionally switch teats while nursing at the *baseline* flow rate and I expected them to increase their sampling frequency when milk-flow rate was slower because in this case, it would be important to find a more profitable teat to increase milk intake.

1.8 Motivation

When an animal performs a behaviour, it is acting on an internal state called motivation. Generally, when an organism is faced with a stimulus, a motivational state is generated and some behaviour is performed in order to reduce this state. There are various models that have been put forth to explain how motivation operates and here I will discuss the general ideas underlying motivational theory introducing the models which are relevant to nursing behaviour.

1.8.1 Stimuli

A motivational state arises as a result of a combination of perceived internal and external factors (de Passillé and Duncan, 1995). Internal factors which are also called "drives" arise from changes in homeostasis, circulating hormones or circadian rhythms. External stimuli, also termed incentives or releasers, elicit behaviour. Drives and incentives have different levels of importance depending on the situation. In the case of escape behaviour, it is the mainly the external stimulus, the feared object, that causes the motivational state of fear. In feeding, however both component factors – hunger and the presence of food – are important to consider.

Behaviours which occur in regular time patterns are difficult to explain in terms of incentives. They seem to emerge predominantly as a result of endogenous factors, possibly due to circadian rhythms. An example of this type of behaviour is environmental patrolling, when an animal abandons other activities to do a routine check of its territory (Toates, 1986; Jensen and Toates, 1993). The motivation for these behaviours increases exponentially since the time they were last performed, but can also be affected by other internal or external factors (Jensen and Toates, 1993; Hogan, 1997). For example, as a result of an external stimulus such as a noise, an animal may patrol its environment earlier than it would normally have.

During a sucking bout, calves teat-switch, butt, teat-strip, and release the teat throughout their meal on the dam (Lidfors *et al.*, 1994) despite any obvious stimulus factor, although milk-flow rate may fluctuate, and decreases are thought to stimulate these behaviours. However, calves butt during a meal sucked through a feeding apparatus when the flow rate is constant (Haley *et al.*, 1998a), so these behaviours may also be released when some internal state of energy reaches a threshold (Hogan, 1997). I hypothesised that calves would be motivated to sample the other teats throughout the meal when flow rate was constant and thus there was no obvious external stimulus.

1.8.2 Fixed action patterns

Fixed action patterns (Lorenz and Tinbergen, 1938) describe situations where animals respond to a given stimulus with a predictable and stereotyped series of behaviours. In a famous experiment, it was demonstrated how the female greylag goose (*Anser anser*) would retrieve an egg which had been rolled out of her nest, by rolling it towards herself with a stereotyped, side-to-side manner. Removal of the egg did not disturb the fixed action pattern when it had already been set in motion. Fixed action patterns are important in maintaining behaviours that are not immediately rewarded or reinforced but that are adaptive (Goodenough, 1993).
Calves' high switching and butting behaviour, which are concentrated at the beginning of a nursing, could also be interpreted as fixed action patterns because they occur at every nursing, even in the absence of the cow. Calves can be observed to butt and attempt to "switch" when they are drinking from a bucket of milk. The complete natural stimulus is not always required to elicit a fixed action pattern. As long as an important component of the stimulus is presented, the behaviour will be released. For example, when calves are motivated to suck, many objects will act as releasers for this behaviour, including objects in their enclosures and parts of their pen-mates' bodies.

At the beginning of the meal, there is milk in the cisternae for the calf to access but for milk flow to increase, it is important that the calf stimulate the dam so that milk ejection will occur. Since butting occurs when milk-flow rate is reduced or stopped (Haley *et al.*, 1998a) and teat-switching is thought to occur under these same circumstances, calves would not be motivated to butt or switch teats at the beginning of the nursing since flow rate is not slow. It would therefore be adaptive that the calf perform these behaviours as a result of fixed action patterns,

in the absence of a reduced milk-flow rate. I wanted to test the hypothesis that calves would teat-switch at a high rate in the first minute of the meal when milk-flow rate was constant and not flowing at a reduced rate.

1.8.3 Positive feedback

Positive feedback has been proposed as a mechanism which maintains a behaviour. In other words, once an animal engages in a behaviour, it has a tendency to persist in that behaviour for some time (Wiepkema, 1971; Toates, 1986; Jensen and Toates, 1993). The concept of positive feedback is important because of a conceptual problem that arises when two motivations, which are of similar importance and strength, occur simultaneously. For example, consider an animal that is both hungry and thirsty and whose motivations to drink and to feed are of about the same importance. Upon the presentation of both food and water, if the animal is slightly more motivated to feed, it starts eating. As it does so, it reduces its feeding motivation so its thirst motivation becomes stronger. According to theory, it should then switch over to drinking. If it then drinks, it reduces its thirst motivation until its feeding motivation becomes stronger. In a situation such as this, if the activity the animal was engaging in was solely governed by the strength of the motivation, the animal would be switching back and forth, from one activity to another (Rushen *et al.*, 1993), but this is not what is observed and it would be inefficient for the animal to behave in this manner. Positive feedback ensures that an animal persists in performing just one behaviour at a time.

Positive feedback is an important concept in understanding nursing behaviour because it ensures a calf will continue to nurse once it has begun and will not be distracted into doing another activity. It may also be why calves have been described as showing a teat preference (Horrel, 1993; Mayntz, 1996). In reality, a calf may remain on a given teat merely because it began on that teat, not because it prefers it.

1.8.4 Teat preference

Each of the four teats of the udder drains a separate mammary gland and calves tend to show teat preferences (Horrel, 1993; Mayntz, 1996) which have been reported to be for the two anterior ones (Hafez and Lineweaver, 1968; Selman *et al.*, 1970; Edwards and Broom, 1982;

Lidfors, 1994). This preference may be because the anterior half of the udder produces 20% more milk than the posterior half (Hurley, 1998) or because sucking the anterior teats distances the calves from the legs of the dam thus reducing their chances of being kicked. The increased milk production of the anterior quarters may be the result rather than the cause of the more frequent sucking since the frequent milking of a gland increases milk production in that gland, independently of the other glands (Svennersten *et al.*, 1990). Having a teat preference could have an effect on teat-switching behaviour by rendering a switch away from a favourite teat less likely than a switch towards a favourite one.

The hypothesis I tested was that calves would indeed spend more time on one teat than on the other but that the teat chosen would not always be the same for a given calf since both teats delivered the same flow rate and they were not feeding from a cow. This prediction would be correct if the principle operating were positive feedback. If calves actually preferred one teat over the other, it would be expected that the calf would always spend more time on the same teat.

1.9 The motivation to suck

Sucking motivation has been extensively studied by observing calves sucking non-nutritive teats. By using this method, different factors could be tested to see how these factors affected calves' motivation to suck without results being complicated by the calves' motivation to obtain milk and thus feed. The taste of milk is a strong stimulus for sucking and as little as 20 ml stimulated calves to suck on non-nutritive objects within their enclosures, the body parts of pen-mates or an artificial rubber teat (Caza *et al.*, 1993; Rushen and de Passillé, 1995; de Passillé and Rushen, 1997). This effect increased as the concentration of milk replacer increased (de Passillé *et al.*, 1997). Outside of meal-time, when milk was not available, very little non-nutritive sucking was observed.

Simply removing the taste of milk from the teat by providing calves with a clean, non-nutritive teat did not reduce sucking after the meal. Attempting to rinse the taste of milk from calves' mouths by giving them 100 ml of water after their meal did not affect post-prandial sucking either. However, when offered 1 litre of water after their meal, all calves drank some water and half consumed the entire litre and sucking by the calves finishing the litre of water continued

for 20 to 40 seconds afterwards (non-nutritive sucking). This time spent non-nutritive sucking was 60% reduced compared to when no water was given, but if the time spent sucking for the water was considered to be non-nutritive and thus added on, overall post-meal sucking was not reduced. This result indicates that either the dilute taste of milk in half of the group's mouths was still stimulating sucking or that once the calves had tasted milk, a certain amount of sucking had to be performed before the motivation to suck waned. It is possible that calves are innately motivated to always do a small amount of non-nutritive sucking after the flow of milk stops to ensure that the dam's udder is well drained (Gaboury and de Passillé, 1997).

The length of the meal affected the amount of sucking calves did to finish their milk as well as how much sucking they chose to do afterward. In an experiment where the resistance to milk flow was varied, at flow rates of 0.30 l/min and faster, after sucking for the duration of their meals calves spent 4-5 min sucking a non-nutritive teat. As the flow rates decreased, the calves had to apply a greater negative pressure to suck their milk but were nevertheless able to maintain a constant meal length. Only at a very-slow flow rate (0.13 l/min) were calves not able to compensate and as a result meal length tripled. Following this longer meal, the post-prandial sucking reduced to 2 minutes demonstrating that spending more time sucking for a meal reduced calves' motivation to suck after the meal (Haley *et al.*,1998b).

Similarly, Ohrberg and Lidfors (1999) showed that the rate at which milk could be drunk had an important effect on post-meal, non-nutritive sucking. Meals that lasted 15 minutes resulted in calves doing less sucking after their meals than calves that had only spent 3.5 minutes drinking. This finding was true whether the calves drank directly from a bucket or sucked milk from a teat. The fact that the post-meal sucking still persisted after calves had sucked milk for 15 minutes demonstrates the importance of sucking and that sucking motivation does decrease although it does not disappear when calves spend increased time consuming their meal. However, after thirty minutes had passed since calves have tasted milk, sucking motivation waned whether calves had sucked or not, possibly due to circulating digestive hormones such as insulin (Marchini *et al.*, 1987; de Passillé *et al.*, 1993) which are thought to play a role in satiety (de Passillé and Rushen, 1997).

Calves chose to eat a handful of hay over performing non-nutritive sucking after they had consumed their milk, but at the beginning of the meal, they preferred to suck their nutritive

teats over eating a handful of hay. Merely distracting calves with the sound of ruffling hay or by showing them a handful of hay after the meal did not reduce their motivation to do non-nutritive sucking although it momentarily caught their attention (Gaboury and de Passillé, 1997).

Non-nutritive sucking has received much attention because it can be directed at inappropriate objects such as the body-parts of pen-mates (Caza *et al.*, 1993; Lidfors, 1993). Calves that did non-nutritive sucking after the meal seemed particularly attracted to sucking teat-shaped objects (Hoyer and Larkin, 1954; Metz, 1984; Caza *et al.*, 1994) and objects which released fluid (de Wilt, 1985; Gaboury and de Passillé, 1997).This type of sucking is believed to have a negative effect on health and production (Wiepkema *et al.*, 1983). The calf being sucked becomes vulnerable to skin injury and infection (Sambraus, 1980), and the calf doing the sucking often ends up drinking urine (de Wilt, 1985) which can result in reduced weight gain (Hafez and Lineweaver, 1968). Calves that sucked for their meals are less likely to suck objects in their enclosure after a meal than calves that had not sucked (Caza *et al.*, 1994; Rushen and de Passillé, 1995).

In conclusion, the motivation to suck is not necessarily a by-product of the motivation to eat and is not satisfied by the simple ingestion of milk, although it is not totally independent of hunger. Increasing the amount of milk calves had drunk did not decrease the ensuing non-nutritive sucking, but having them skip a meal caused the duration of non-nutritive sucking at the next meal to increase (Rushen and de Passillé, 1995; de Passillé and Rushen, 1997).

1.10 The motivation to butt

In addition to sucking, the taste of milk also stimulated butting (Caza et al., 1994; Rushen and de Passillé, 1995). Butting occurs during both natural (Lidfors *et al.*, 1994) and artificial nursings (Haley *et al.*, 1998a; Pan, 1993). As with the high-frequency butting that occurs right at the beginning of the meal, butting during the meal does not require the presence of the dam's udder. Calves butted at their buckets or at artificial teats following milk intake (Haley *et al.*, 1998a). By contrast, calves did not butt when sucking water from an artificial teat, (Gaboury and de Passillé, unpublished data) or after drinking water from a bucket (de Passillé *et al.*, 1992).

A reduced flow rate motivates calves to butt. Lidfors (1994) observed calves on dairy cows which have more milk in their cisternae and found that their meal durations were shorter and there was less manipulation and butting than by calves on lower-producing beef cows. Edwards and Broom (1982) also observed that calves nursing heifers spent more time butting the dams' udders and switched teats more than did calves of multiparous cows reflecting the fact that heifers have less milk available than multiparous cows. De Passillé *et al.* (1996) demonstrated that calves sucking on cows that had been totally milked a half hour before the meal and thus had less milk available butted 6 times more than those on cows that had only been partially milked.

Since it is difficult to measure flow rate from the udder, Haley *et al.* (1998a) devised a feeding apparatus which allowed them to manipulate the rate of milk flow as the calf was feeding. They demonstrated that calves butted less (0.6 butts/min) when milk was delivered at a rate of 1.33 l/min than when it flowed at 0.14 l/min, which elicited twice as many butts per minute. Stopping the flow for 30 seconds dramatically increased butting from 0.2 to 5.2 butts/min. Increasing the flow rate did not cause a change in butting frequency, indicating that butting did not simply result from a change in milk-flow rate, but from a reduction in flow rate. Similarly, at the end of the meal when milk flow stopped, calves again responded by butting and this response was greater (7 butts/min) than when milk was stopped during feeding. The response diminished with each consecutive minute thereafter. Haley *et al.* (1998a) concluded that an increase in the butting of ungulates during a nursing is a reliable indicator that milk flow has waned or stopped and it may be indicative of periods of non-nutritive sucking. It seems reasonable that a slow milk-flow rate would result in an increase in butting since butting has been suggested to stimulate the milk-ejection reflex, and thus increase milk-flow rate.

1.10.1 The mechanical-tap stimulus

Although it seems feasible that stripping, teat-releasing and even teat-switching may act to stimulate the milk-ejection reflex, butting is such an abrupt and rough movement that it seems reasonable that it might have some additional functions. It has been suggested that butting may stimulate milk flow by acting as a 'mechanical-tap stimulus' causing the myoepithelium to contract independently from the effects of oxytocin since it was demonstrated that inhibition of the neurohormonal reflex does not affect the mechanical response. The myoepithelium in the

mammary glands of goats, mice, rabbits and rats contracted in response to mechanical stimulation or a sharp tap by a blunt object on the skin of the udder and was not nervous in nature (Cross, 1954; Findlay and Grosvenor, 1967).

Another possibility is that butting might dislodge trapped milk in the udder. In ewes, for example, because the teats are oriented outwards, the centre of the udder forms pockets where milk may become trapped. Butting by the lamb is thought to force this milk into the teat (Marnet[1]). In dairy cows there has been much artificial selection for downward-facing teats and thus the udders do not form pockets. However, the interior of the glands are folded and may trap milk (Mayntz *et al.*, 1996) which could potentially be dislodged by butting. In any case, the calf's behaviour would have evolved before this artificial selection, when teats may have been more oriented outwards.

Having several mechanisms that aid in the milk removal process is adaptive since nursing is so important for the survival of young mammals. It ensures that if one system does not function correctly, there are other, back-up mechanisms (Lefcourt and Akers, 1966).

1.11 The motivation to switch teats

When calves have more than one teat available, such as when they are sucking their dams, they commonly switch among teats (Lidfors *et al.*, 1994). A reduced flow rate may motivate teat-switching since this behaviour occurs at the end of a sucking bout on a teat, when there is thought to be a reduced flow rate from the udder. I wanted to investigate whether calves would increase teat-switching frequency when milk-flow rate was constant but reduced.

As the nursing progresses, and presumably the milk available in each teat diminishes, calves spend less and less time on each teat, switching more and more frequently (Hafez and Lineweaver, 1968; Mayntz *et al.* 1996). In support of this idea, Lidfors (1994), observed that in contrast to beef calves, dairy calves terminated their meals before they had sucked from all 4 of their mothers' teats. Edwards and Broom (1982) found that new-born calves sucking lower-producing heifers, made an average of 8.7 teat-switches during a nursing. By contrast,

1) Personal communication, May 1997.

calves on higher-producing dams only switched an average of 2.9 times. Heifers were also more likely than older cows to move around and thus interrupt their calves during a nursing (possibly due to the high rate of butting) therefore a higher incidence of teat-switching may have resulted from the more frequent movements of the mother (Edwards and Broom, 1982). More evidence that switching is related to milk production was demonstrated by Petit (1972) who reported that teat-switching increased in autumn when cows produced less milk.

Teat-switching tends to occur around the same time that butting does, supporting the idea that the two behaviours are motivated by the same stimulus. Since it has been shown that butting is stimulated by a decrease in milk-flow rate (Haley *et al.*, 1998a), I was interested in testing whether teat-switching was also motivated by a sudden decrease in flow rate and how the magnitude of the reduction affected the response. I also wanted to see whether having a second teat that was non-nutritive instead of nutritive would have an effect.

1.12 Hypotheses

The main hypotheses I set out to test in this study were the following:

When calves had 2 teats,

- overall teat-switching, butting, releasing and stripping would increase at decreased milk-flow rates;
- calves would teat-switch, butt, release the teat and teat-strip more frequently at the beginning of the meal, regardless of milk-flow rate;
- teat-switching, butting, teat-releasing and teat-stripping would occur at lower frequencies throughout the meal in the absence of changes in milk-flow rate;
- during the meal, a sudden decrease from the *baseline* milk-flow rate would result in butting, teat-releasing and teat-stripping and ultimately a teat-switch and The overall frequency of this response over repeated trials would be greater when the magnitude of the reduction is higher;
- during the meal, a sudden decrease from the *baseline* milk-flow rate would result in a teat-switch following the reduction;

- the decision to switch teats was based on the status of the teat being sucked and therefore, calves would behave as predicted even when the second teat was non-nutritive;
- calves would demonstrate a teat preference measurable in terms of the duration spent on each teat but the "preferred" teat would not be constant from meal to meal.

CHAPTER 2
MATERIALS AND METHODS

2.1 Animals and housing

Sixteen male Holstein calves (10 ± 3 days old) were bought on March 15, 1996 from local producers and housed eight to a room. Each group shared its room with eight other calves bought at the same time and of the same age. Calves were cared for according to the recommended codes of practice. Procedures were approved by the institutional animal care committee which follows the guidelines of the Canadian Council for Animal Care (Agriculture Canada, 1988).

Each room contained four rows of six pens (2.1 × 1.85 m) with an alley running down the centre and along the four walls of the room. The fencing of the pens consisted of vertical iron bars which allowed some contact between neighbouring animals as well as a full view of the room. Each calf had 3 neighbours within contact, one on the side and two at the back. The cement floor was covered in wood shavings which were changed daily at 0600h. Lights were on from 0600h to 1800h. The rooms were ventilated and ambient temperature varied with the temperature outdoors, but was not allowed to drop below 20°C. Relative humidity was maintained between 60 and 70%. Affixed to the side of the pen facing the aisle, was a metal bucket holder and two metal teat supports 61.0 cm from the floor and 38.1 cm apart.

2.2 Feeding

Calves were fed a commercial milk replacer (Lacvor Élevage, 20% crude protein, 18% crude lipids) at 39 ± 1 °C, and according to the company-recommended quantities (Appendix A). Meal quantities were never increased during an experiment. Milk meals were given at 0700h and 1500h, using the single-teat feeding apparatus based on Haley et al. (1988a) (Figure 2). Hay

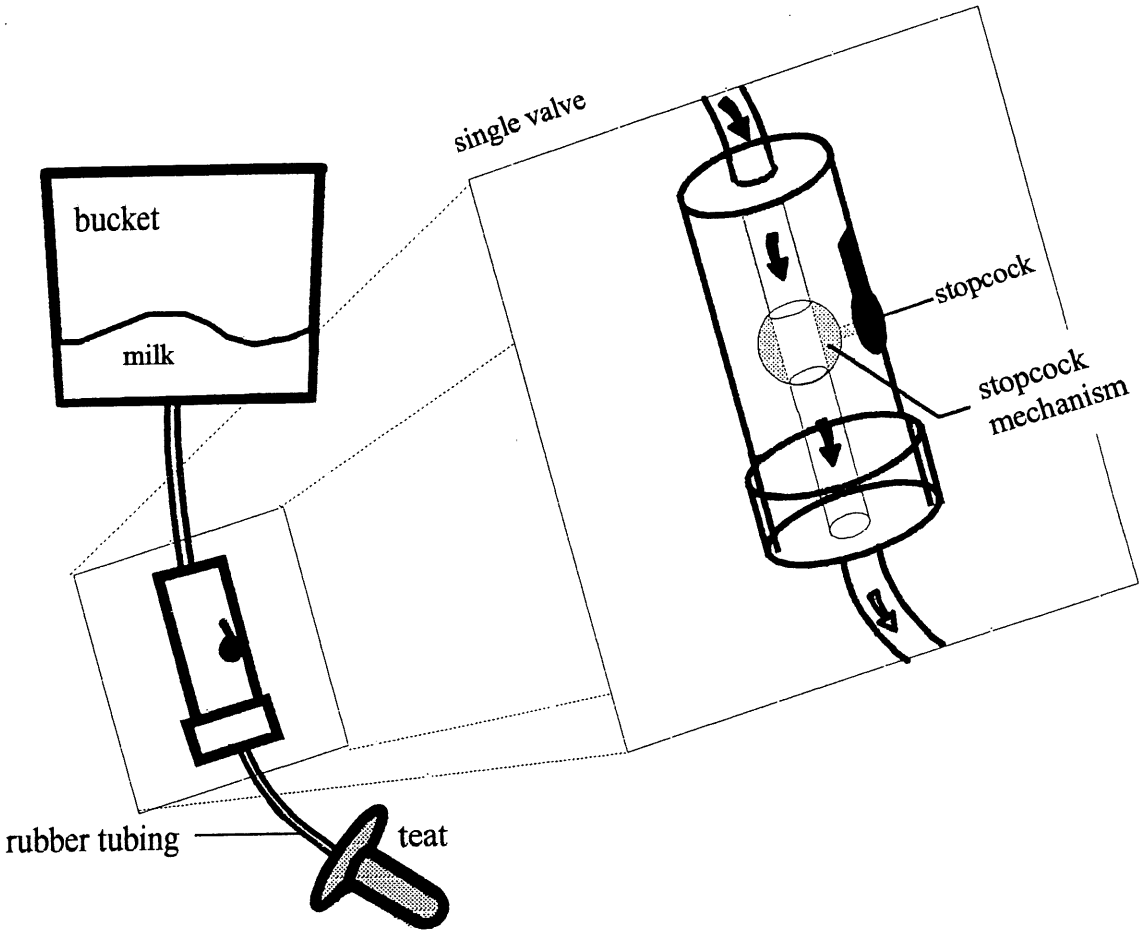

Figure 2. Single-teat feeding apparatus with an enlarged view of the valve

supplemented the diet and was placed on the floor, just outside the calf's pen, after 1600h, daily (Appendix A). Calves were weighed every 2 weeks to monitor weight gains. Water was given *ad libitum* except for 2 hours prior to each weighing.

2.3 Single-teat feeding apparatus

This feeding apparatus was used for all the non-experimental meals as well as for Experiment 1. The bucket containing the milk was in a support at a height of 61.0 cm from the floor and was tilted at 15° to facilitate drainage. The milk travelled via plastic tubing and exited through a rubber teat that the calf could suck on (C. A. L. F. Sucklers, Milk Specialties Co., Dundee, Illinois: length: 10 cm; diameter: 2 cm; wall thickness: 0.4 cm), (Figure 2). The teats had two perpendicular cuts which opened into a 0.3 cm hole when the teat was compressed. The teats were held in a horizontal position by the teat support. A stopcock was fitted to the tubing so that when the calf finished its milk, the stopcock could be shut to prevent air-sucking which can lead to bloating and also to stop extra drops of milk from flowing into the teat. The total length of the tube and stopcock was 107 cm, and the smallest point of the feeding apparatus had a diameter of 0.34 cm resulting in a milk-flow rate I called *baseline* for the purpose of these experiments (Table 3).

2.4 Feeding protocol

Calves were fed in the same order at every meal. Milk was poured into all the buckets which were placed in the bucket-holders. Once all of the buckets were filled, the teats were placed in the teat holder closest to the bucket, in the same order as above, and the calves could start drinking. When the calves finished drinking, the valves were shut off and the teat was left in place for 15 minutes, to allow the calves to perform non-nutritive sucking without swallowing air or droplets of milk from the tubing (de Passillé *et al.*, 1992).

2.5 Double-teat feeding apparatus

This feeding apparatus (Figure 3) was used for Experiments 2 to 6. The double-teat feeding apparatus was essentially the single-teat feeding apparatus modified in the following way: the stop-cock was replaced with a T-connector to split the stream of milk so that each stream then flowed into its respective Y-valve. The right sides of each Y-valve was fitted with the baseline perforated rubber washer and the left sides were fitted with a rubber washer with a smaller perforation (Figure 4), according to the treatment being given (Table 3). By changing the position of the valve's stopcocks we could manipulate flow rate by diverting the milk flow through either washer. As a result milk-flow rate was controlled in the corresponding teat. (Figures 3 and 4).

Table 3. Washer perforation diameters and the resulting flow rates[1]

Flow-rate name	Diameter of hole (cm)	Flow rate (l/min)
baseline	0.34	0.66
slow	0.24	0.46
very-slow	0.16	0.20
extremely-slow	0.08	0.04
off	0	0

1. determined by letting 2 l of water flow through the feeding system with the teats removed

2.6 Experimental procedure

Experiments began when the calves were 13 weeks. As two calves died prior to starting experiments, only 14 calves were used. Until then, calves had only drunk from one teat which had always been placed in the same teat support. In order to prepare them for the two-teat experiments, during non-experimental meals two weeks prior to the experiments, the location of

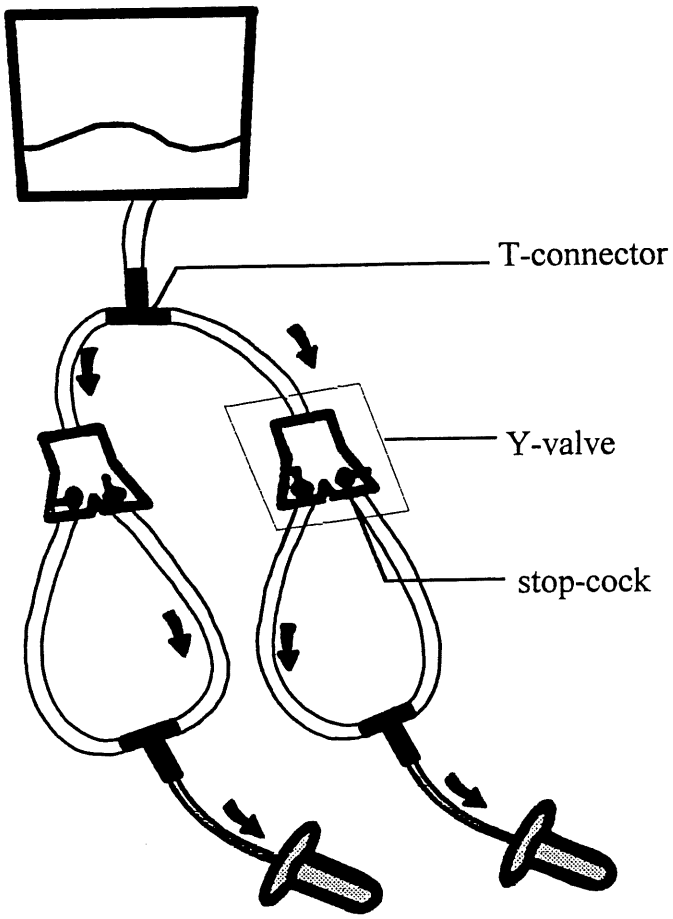

Figure 3. Double-teat feeding apparatus with arrows indicating the milk flow.

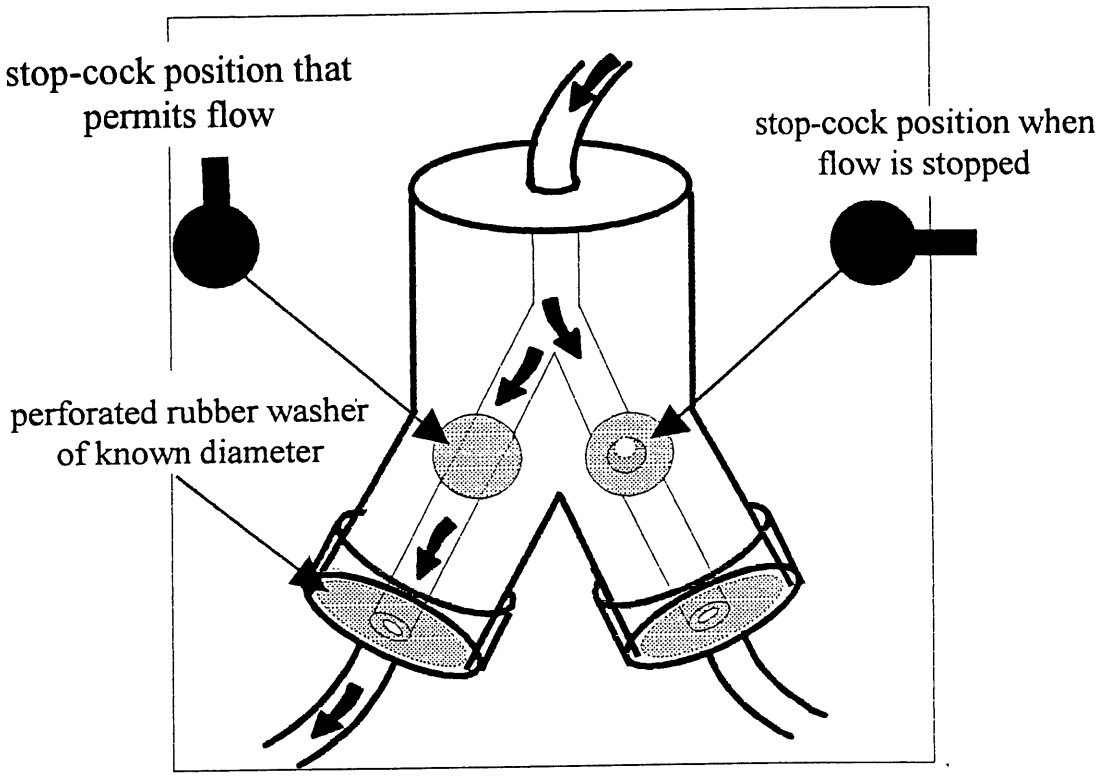

Figure 4. Enlarged view of the Y-valve with arrows indicating flow diversion. Stop-cocks are drawn above to show how their position diverts the flow. The diameter of the hole in the washer determines the flow rate.

the teat was systematically alternated between supports, on a daily basis. Therefore, calves experienced drinking from a teat placed in either support.

Since the calves had never had access to two teats, one week prior to the experiments, we set up a training session whereby the calves were fed using the double-teat feeding apparatus. We observed the calves to see whether they would teat-switch. If after five minutes, a calf had not yet drunk from the second teat, we encouraged it to do so by tapping the teat with our fingers and calling the calf. By the end of the meal, all calves had drunk from both teats.

All experiments were performed during the morning meal. Experiments having 4 treatments lasted 4 days and those with 3 lasted 3 days. Treatment orders were balanced so that each calf received one treatment per day and every calf experienced all the treatments, making the calf its own control (Table 4).

Table 4. Treatment orders for experiments with 3 and 4 treatments

Calf	3 Treatments			4 Treatments			
	Day 1	Day 2	Day 3	Day 1	Day 2	Day 3	Day 4
W	-	-	-	A	B	C	D
X	A	B	C	D	C	B	A
Y	C	A	B	B	A	D	C
Z	B	C	A	C	D	A	B

Calves were video taped (Panasonic WV - BL200; Panasonic, Secaucus, New Jersey) from the side, during all experiments (Figure 5). Four-way video splitters (Uniplex Sprite Video Multiplexer; Dedicated Microcomputers Ltd, Reston Virginia) enabled us to simultaneously and continuously record (Panasonic AG - 6730; Panasonic, Secaucus, New Jersey, 2-h mode) four

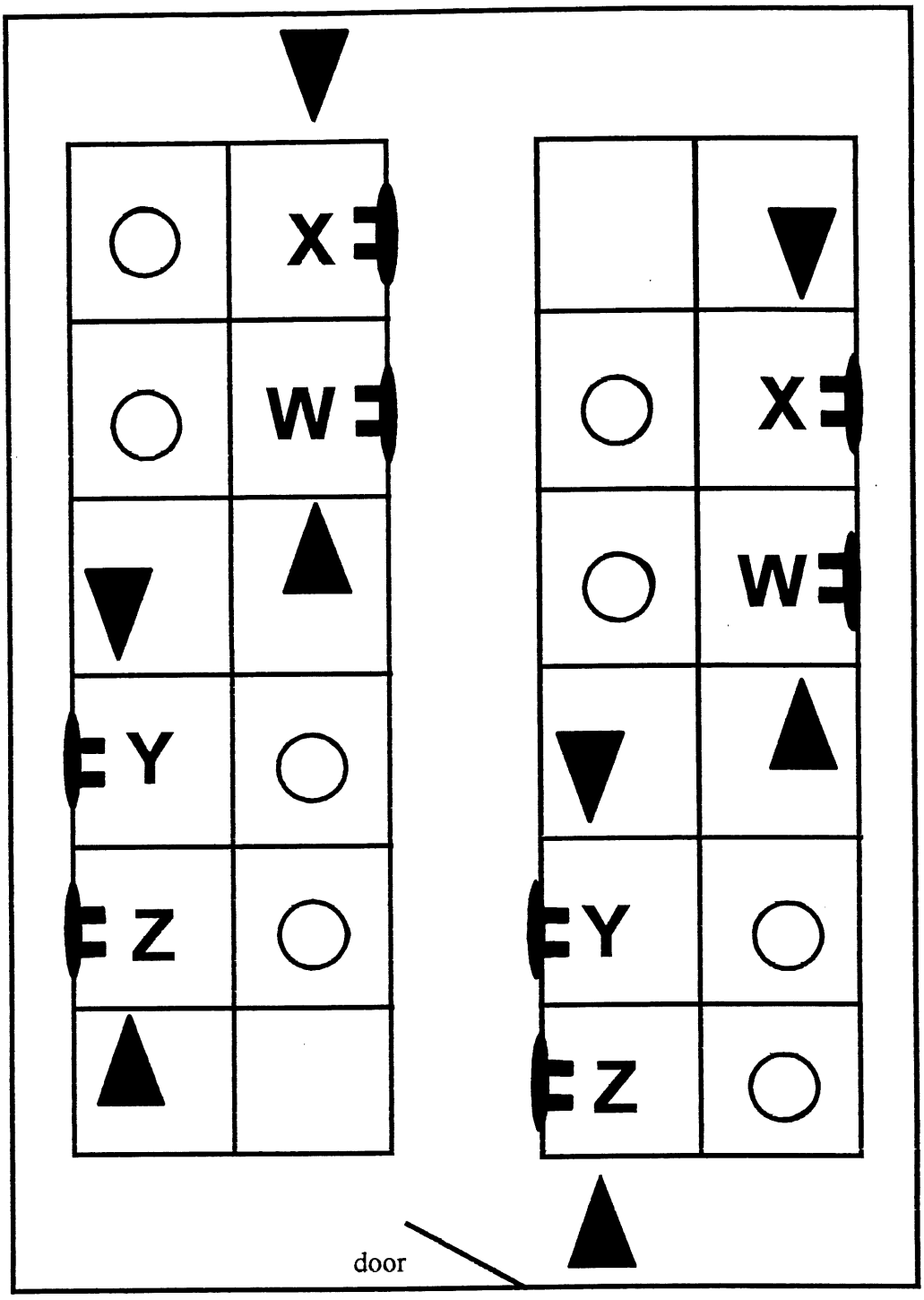

Figure 5. Diagram of filming set-up of one of the rooms. Each calf is represented by a letter, each camera by a triangle and each feeding apparatus by an ellipse (the small, black rectangles are the teats). Calves from another project are represented by open circles.

calves onto the same cassette. The calf's head and neck and the teat the calf was sucking could be seen on the monitor. Using *The Observer* computer software (Noldus Information Technology), the videos were watched using continuous sampling to score behaviours based on the definitions that follow. The teat the calf was sucking was identified as either being near or far from the camera so the teats could be differentiated between and also to determine the time spent on each one.

Sucking duration - far teat: Time the teat farthest from the camera was in the calf's mouth, unbent, for at least 3 seconds and the calf was opening and closing its mouth rhythmically.
Sucking duration - near teat: Time the teat nearest the camera was in the calf's mouth, unbent, for at least 3 seconds and the calf was opening and closing its mouth rhythmically.
Teat-switching frequency: The number of times the calf left the teat it was sucking on to face the other teat (and usually suck on it).
Butting frequency: During sucking, the calf used its head to make an abrupt, vertical movement. The movement could have one or two components: The head was abruptly raised with the body following the motion; or the head was first abruptly lowered, so that the nose was slightly below the teat, and then abruptly raised with the body following the motion. This movement was directed anywhere within a 30-cm radius of the teat. The number of times the calf butted was measured.
Stripping frequency: The number of instances where the calf abruptly slid its mouth from the base to the tip of the teat, its mouth may or may not have momentarily stopped touching the teat, but there was absolutely no pause in the movement.
Releasing frequency: The number of times the calf had the teat in its mouth, released it, and returned to it in less than 3 seconds. This was distinguished from stripping in that there was a momentary pause in the movement during the time when the calf's mouth was not touching the teat.
Teat-directed behaviours: The sum of the frequencies of butting, releasing and stripping.
Unknown: Time during which the calf's head and neck were out of the field of vision for more

than 3 seconds so that behaviour could not be observed.

Other: Time during which the calf was performing a behaviour that was not being recorded (i.e. playing).

2.7 Patterning of behaviours at the beginning of the meal

2.7.1 Experiment 1

The purpose of this experiment was to observe the calves' behaviour while they were nursing from one teat. Fourteen calves were fed using the single-teat feeding apparatus and observed drinking at the *baseline* flow rate for the first five minutes of their meal, which was divided into ten 30-second periods.

2.7.2 Experiment 2

In this experiment the calves' behaviour was observed when they were given access to one nutritive and one non-nutritive teat. We measured the overall frequency and initial pattern of teat-switching and teat-directed behaviours. Fourteen calves were observed during the first 2.5 minutes of the meal. (Only the initial 2.5 minutes were available for observation since data were taken from Experiment 6, which is described later on).

2.7.3 Experiment 3

The purpose of this experiment was to observe calves' behaviour when they were presented with two nutritive teats. We were interested in measuring the overall frequency and initial pattern of teat-switching and teat-directed behaviours and how flow rate affected these behaviours (Table 3). Therefore, we used the two extreme flow rates: *baseline* and *extremely-slow* since these had

affected the frequency of butting in previous tests (Haley *et al.*, 1998a). Fourteen calves were presented with two nutritive teats and their behaviour was observed for the first 5 minutes of the meal. The treatments were as follow:

A. Both teats at the *baseline* flow rate
B. One teat at *baseline* and the other at the *extremely-slow* flow rate
C. Both teats at the *extremely-slow* flow rate

In each of Experiments 1, 2 and 3 the observational periods were split into 30-second intervals. The frequencies of each behaviour were analysed in a randomised complete block design using the analysis of variance procedure with repeated measures in time (General Linear Models, Statistical Analysis Systems Institute, 1988). *Calf identity* was the main factor and *interval* was the repeated factor in the model used to determine whether there were differences among sequential intervals. In Experiment 3, *treatment* was included as a main factor, and we also examined the interaction between treatment and interval. When there was a significant overall treatment effect, multiple comparisons were used to compare all possible treatment pairs and the Bonferroni adjustment was applied to maintain the overall α at 0.05 (Kleinbaum *et al.*, 1987). To see if calves had a teat preference, the first teat visited at the beginning of 19 different meals was recorded and the binomial probability distribution was used to determine whether calves were starting on one teat more often than the other (Zar, 1984).

2.8 Experiments in which flow rate was suddenly reduced

In the following 3 experiments we used the double-teat feeding apparatus to reduce the flow rate for 5 seconds in the teat the calf was sucking on. In a pilot study, calves had switched teats following a 6-second reduction in flow rate in 4 out of 5 repetitions but in these experiments I chose 5-second reductions because when calves switched, they usually did so within the first 2

or 3 seconds and also because technically, intervals of 5 seconds were easier to work with. Since the calves acted excitedly (repeatedly butting, releasing and switching) when they first received their milk, we let the first minute of the meal elapse before beginning our tests. Once this minute was over and the calf had settled on a teat for 10.0 seconds, we started the treatments. After a flow-rate reduction we recorded whether or not the calf switched to the other teat. We repeated this procedure five times for each treatment so that the maximum number of switches possible was 5. I also recorded the total frequencies of butting, releasing, stripping and teat-directed behaviours during each of the five five-second periods.

I recorded the exact moment the flow rate was reduced using a hand-held computer with a timer (Psion HC110 programmed using *The Observer* computer software, Noldus Information Technology). Later, when videos were watched to gather behavioural data, having these times allowed me to know how long it took, following a reduction in flow rate, for a particular behaviour to occur (i.e. When I observed a calf switching teats, I knew exactly how many seconds earlier flow rate had been reduced).

2.8.1 Experiment 4

To investigate the behaviour of calves faced with a sudden reduction in milk-flow rate and to examine the effect of the magnitude of the reduction, the calf was presented with two teats delivering milk at *baseline*. When one minute had elapsed, we began the experiment: we made sure the calf remained on the same teat for 10 seconds and then reduced the rate of milk flow from this teat for 5 seconds. The flow was then returned to baseline and this procedure was repeated five times. The treatments were as follows:

A. *baseline* to *baseline* (control)
B. *baseline* to *extremely-slow*
C. *baseline* to off

2.8.2 Experiment 5

This experiment was like Experiment 4, except that I looked at the effect of smaller reductions in magnitude. Treatments were as follows:

A. *baseline* to *slow*
B. *baseline* to *very-slow*
C. *baseline* to *extremely-slow*
D. *baseline* to off

2.8.3 Experiment 6

In this experiment, one of the two teats was turned off for the duration of the experiment and the other delivered milk at the *baseline*. The rest of the experiment proceeded similarly to the previous two: after one minute and once the calf had settled on the nutritive teat for 10 seconds, the milk-flow rate was reduced for 5 seconds and then returned to *baseline*. This procedure was repeated five times. The treatments were as follows:

A. *baseline* to *baseline* (control)
B. *baseline* to *extremely-slow*
C. *baseline* to off

Data during the 10 seconds following the time flow-rate was reduced were analysed because there was a 2-to-3-second delay in the time the reduction in flow rate was recorded and the moment the experimenter actually reduced the flow rate. Therefore, by looking at 10 seconds following the recorded time, I was sure to record all the data occurring during the 5-second reduction period.

I was interested in whether or not the calf would switch teats following a sudden reduction in milk

flow rate, and not in the overall teat-switching frequency during the reduction. Therefore, the only behaviour recorded was whether or not the calf switched to the other teat.

Data were not normally distributed, so the Wilcoxon paired-sample test (Zar, 1984) was used to compare behavioural frequencies among the different treatments. The Wilcoxon signed rank statistic, S, was calculated using the following equation: $S = \Sigma r_1^+ - n(n+1/4)$, where values of 0 were discarded, r_1^+ was the rank of $| x_i |$ and n was the number of x_i (The Univariate procedure, Statistical Analysis Systems Institute, 1988). Since I was making multiple pairwise comparisons, I used the Bonferroni adjustment to maintain α at 0.05 (Kleinbaum *et al.*, 1987). As a result, for differences to be considered significant when there were 3 treatments and thus 3 pairwise comparisons, P had to be less than 0.0167 and when there were 4 treatments and thus 6 pairwise comparisons, P had to be less than 0.0083.

CHAPTER 3
RESULTS

3.1 Patterning of behaviours at the beginning of the meal

This section will describe teat-switching, butting, teat-stripping and teat releasing during the beginning of the meal when calves had one nutritive teat (Experiment 1); one nutritive and one non-nutritive teat (Experiment 2) and finally, when they had two nutritive teats (Experiment 3). All nutritive teats delivered milk at the *baseline* flow rate.

3.1.1 Experiment 1

During the first 5 minutes of the meal, calves sucking on one teat at *baseline* butted twice per minute (Figure 6a) and stripped the teat twice per minute (Figure 6b). They never released the teat (Figure 6c) unless they were butting or stripping. Butting frequency did not differ among 30-second intervals (ex. 1^{st} and 2^{nd} intervals: $F = 0.14$, $P = 0.71$). Since the frequencies of stripping and releasing were never normally distributed, these variables were not independently analysed in any of the experiments. However, since stripping and releasing can appear to be butts of a lesser intensity, the distinction between these behaviours may have been artificial so the behaviours were grouped together as "teat-directed behaviours". The overall frequency of "teat-directed behaviours" (Figure 7a) was 3.5 times per minute on average, and there were no differences among consecutive interval pairs ($F = 1.25$, $P = 0.30$).

3.1.2 Experiment 2

When calves had one nutritive teat at *baseline* and one non-nutritive teat, calves butted

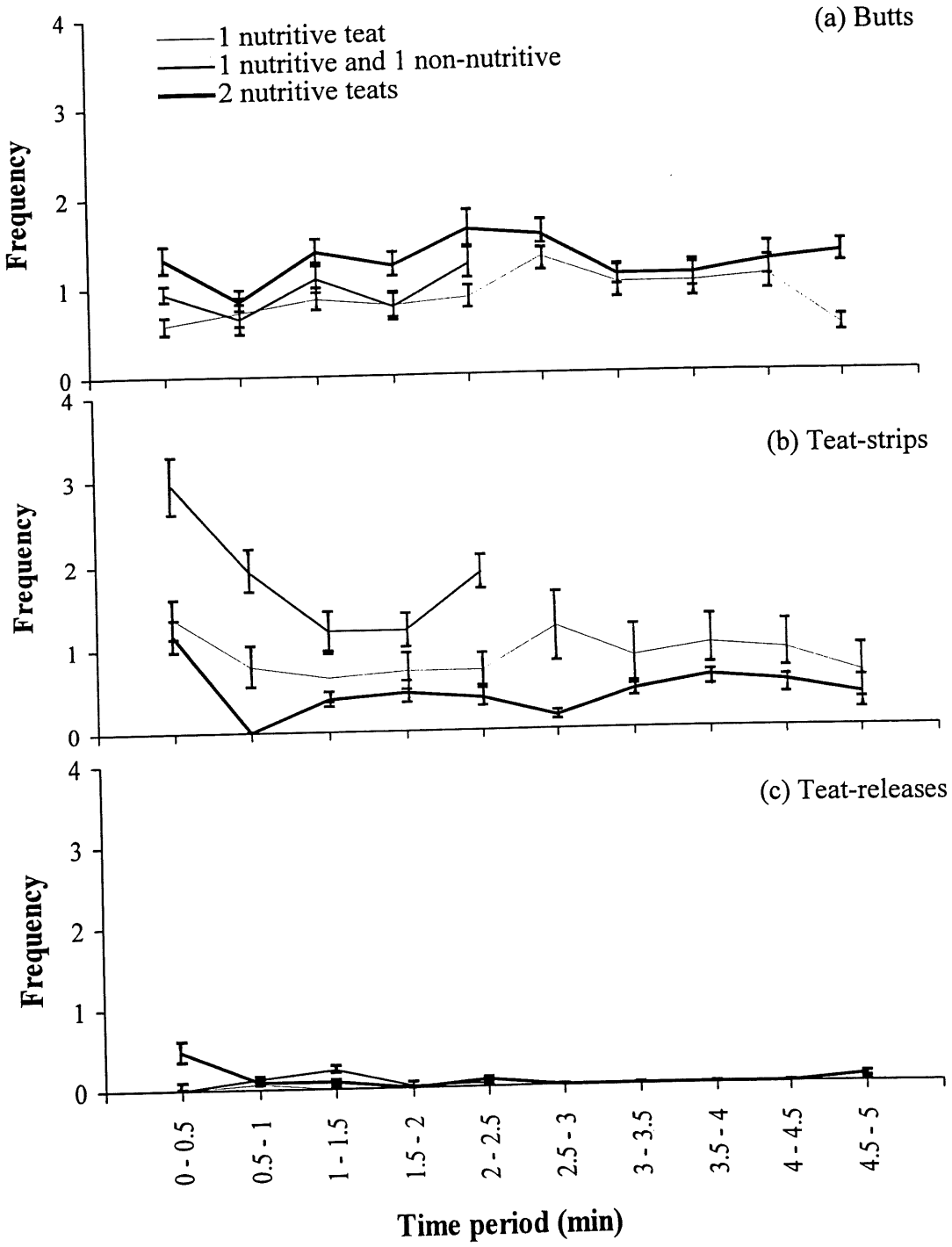

Figure 6. Patterning of events through time when calves had 1 nutritive teat (Exp. 1); 1 nutritive and 1 non-nutritive teat (Exp. 2); and when they had 2 nutritive teats (Exp. 3) to suck from. Mean (± standard error) number of (a) butts (b) teat-strips (c) teat-releases by calves during the first minutes of the meal at the *baseline* flow rate (n = 14).

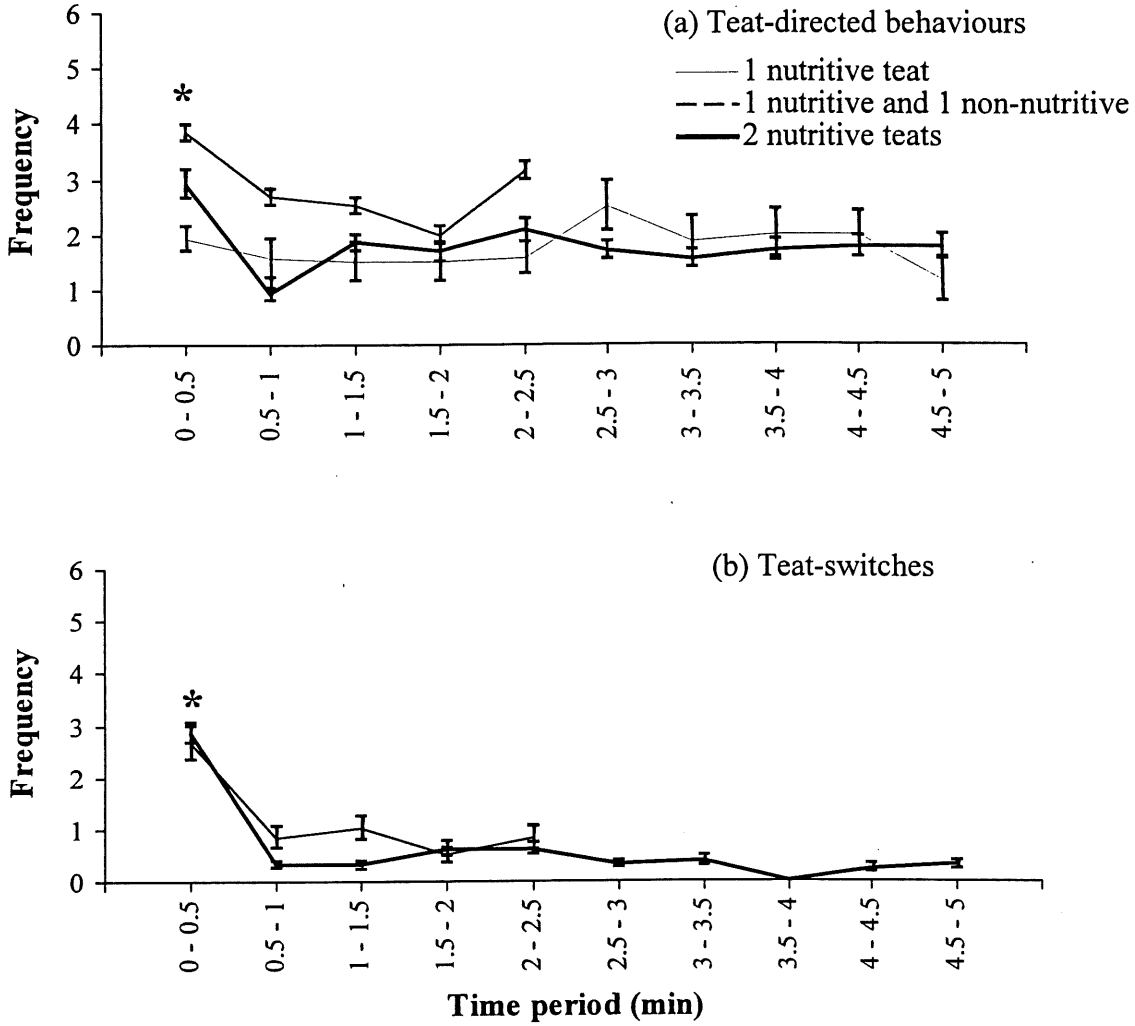

Figure 7. Patterning of events through time showing the higher level of activity in the first 30 seconds of the meal at the *baseline* flow rate when calves had 1 nutritive teat (Exp. 1); 1 nutritive and 1 non-nutritive teat (Exp. 2); and when they had 2 nutritive teats (Exp. 3) to suck from. Mean (± standard error) number of (a) teat-directed behaviours and (b) teat-switches at the beginning of the meal (n = 14). An asterisk denotes a significant difference with the next time period which applies to all the treatment curves. Data were analysed using analyses of variance with repeated measures.

approximately twice per minute, with no differences between 30-interval pairs (Figure 6a, F = 0.87, P = 0.36). Calves stripped the teat about 3.5 times per minute (Figure 6b) and barely ever released the teat (Figure 6c). Overall, teat-directed behaviours occurred approximately 5 times/minute (Figure 7a) and they were more frequent in the first 30 seconds of the meal compared to the next intervals (F = 18.6, P = 0.0001). Calves teat-switched 6 times per minute in the first 30 seconds of the meal and reduced this frequency to once per minute during the next 2.5 minutes (Figure 7b, F = 23.9, P = 0.0001).

The presence of a second teat resulted in an increase in overall teat-directed behaviours and teat switching. In addition, the test revealed that the frequency of teat-directed activity and of teat-switching were higher in the first 30 seconds of the meal than in the subsequent 30-second intervals.

3.1.3 Experiment 3

When the calves were drinking from two nutritive teats at *baseline*, they butted about 2.5 times per minute (Figures 6a and 8a) and this behaviour was relatively constant through time (F = 0.23, P = 0.64). Calves also stripped the teat once per minute (Figures 6b and 8b) and almost never released it (Figures 6c and 8c). "Teat-directed behaviours" in the first 30 seconds were twice as frequent as during subsequent intervals (Figures 7a and 9a, F = 20.8, P = 0.0001). Switching occurred about once per minute during the first 5 minutes of the meal, except for during the initial 30-second interval, during which calves switched teats 6 times per minute (Figures 7b and 9b, F = 101.8, P = 0.0001).

Table 5 gives a descriptive summary comparing the results from Experiments 1, 2, and 3 to show the following tendencies: Calves did about the same levels of teat-switching both in the first interval and overall when two teats were available, regardless of whether or not one of these teats

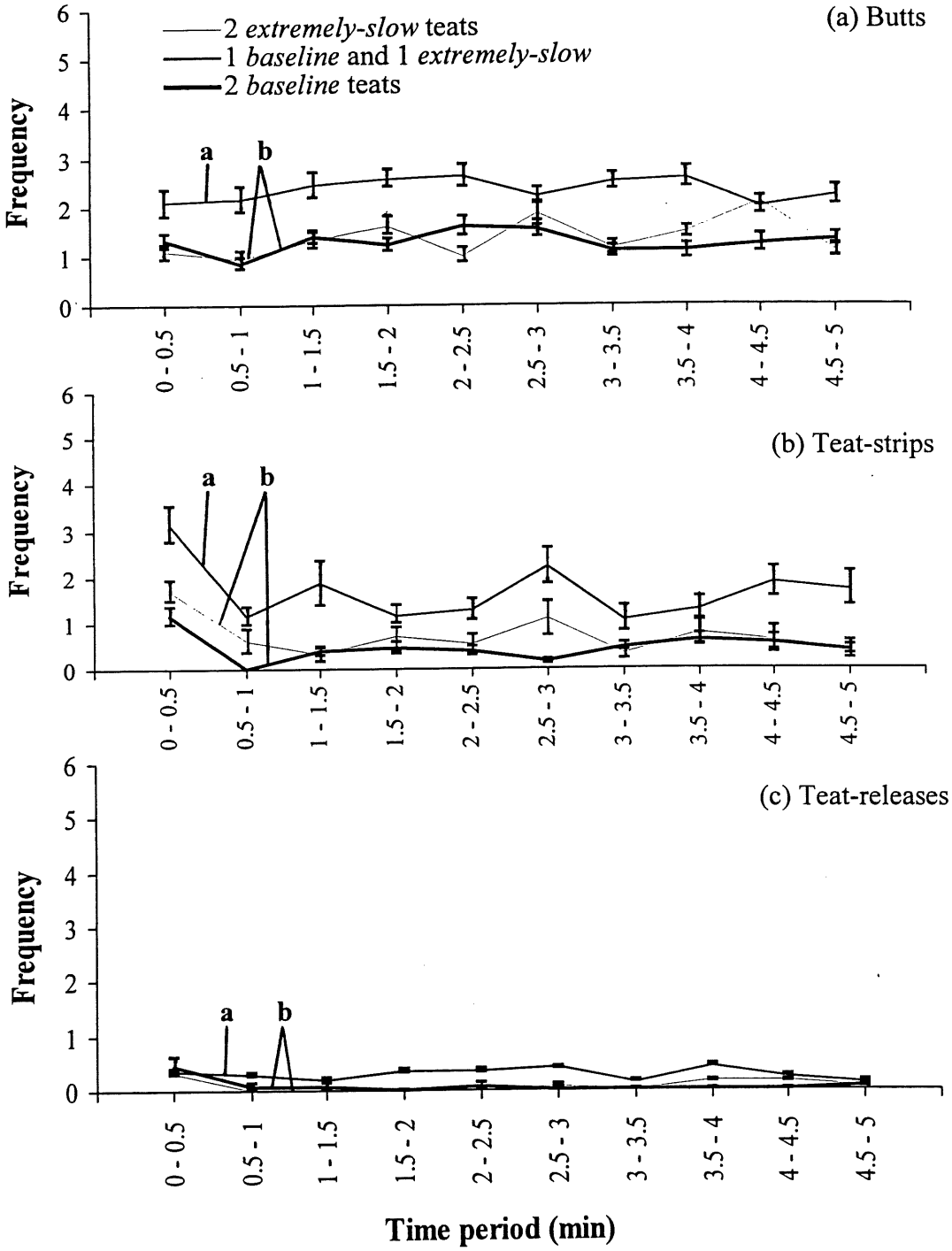

Figure 8. Patterning of events through time when calves were drinking with 2 nutritive teats at different flow rates (Exp. 3). Mean (± standard error) number of (a) butts (b) teat-strips (c) teat-releases during the first 5 minutes of the meal (n = 14). Curves with different letters differ significantly based on analyses of variance with repeated measures.

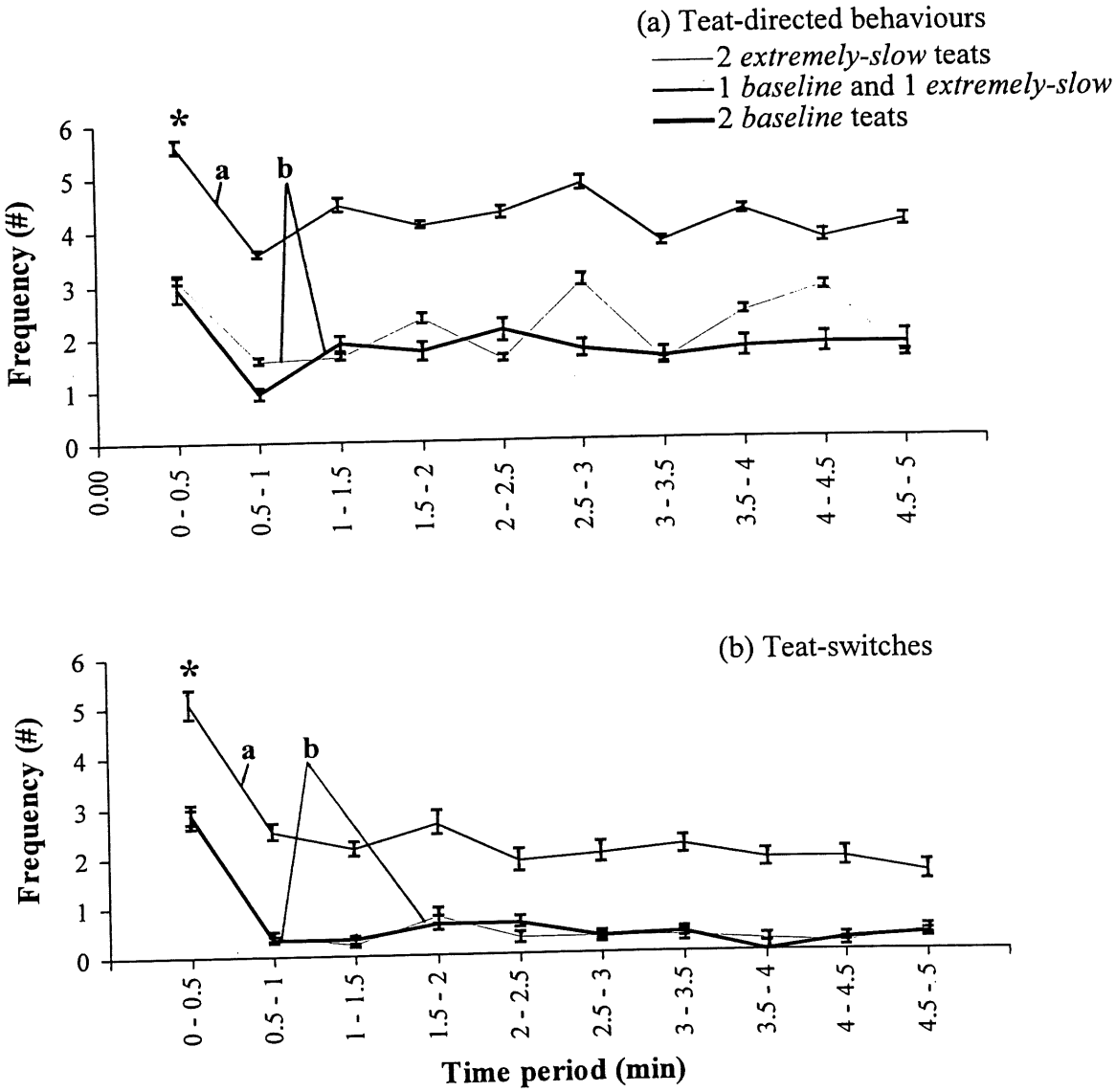

Figure 9. Patterning of events through time when calves were drinking with 2 nutritive teats at different flow rates (Exp. 3). Mean (± standard error) number of (a) teat-directed behaviours and (b) teat-switches during the first 5 minutes of the meal (n = 14). Curves with different letters differ significantly. An asterisk denotes a significant difference with the next time period which applies to all the treatment curves. Data were analysed using analyses of variance with repeated measures.

was nutritive or dry. Butting was relatively constant throughout the three experiments. Calves did the highest amount of stripping when 2 teats were available but one was dry and the least amount when they could drink from 2 nutritive teats. The teats were practically never released during each of these experiments. Teat-directed behaviours followed the same pattern as teat-switching in both treatments where calves had 2 teats available, being very frequent in the first thirty seconds of the meal and then decreasing significantly for the remainder of the 5-minute observation period. This pattern was not observed when the calf had only 1 teat.

Table 5. Summary of results of Experiments 1, 2 and 3 at the *baseline* flow rate

	1 nutritive teat (Exp. 1) (average freq/min)	1 nutritive teat, 1 dry teat (Exp. 2) (average freq/min)	2 nutritive teats (Exp. 3) (average freq/min)
Switching (1st interval)	–	6	6
Switching (overall)	–	1	1
Butting (overall)	2	2	2.5
Stripping (overall)	2	3.5	1
Releasing (overall)	0	0	0
Teat-dir. beh. (1st int.)	3.5	8	6
Teat-dir. beh. (overall)	3.5	5	3

Milk-flow rate had a significant effect on behaviour. Overall, when calves were presented with two *extremely-slow* teats which delivered milk at a rate 16.5 times slower than *baseline*, they switched teats 4 times more (9b, S = -39, P = 0.0005); butted twice as much (Figure 8a, S = -43.5, P = 0.001); stripped three times as frequently (Figure 8b, S = 0.039, P = 0.0005) and increased their releasing behaviour from 0 times per minute at *baseline* to about once per minute at *extremely-slow* (Figure 8c, S = -29, P = 0.020).

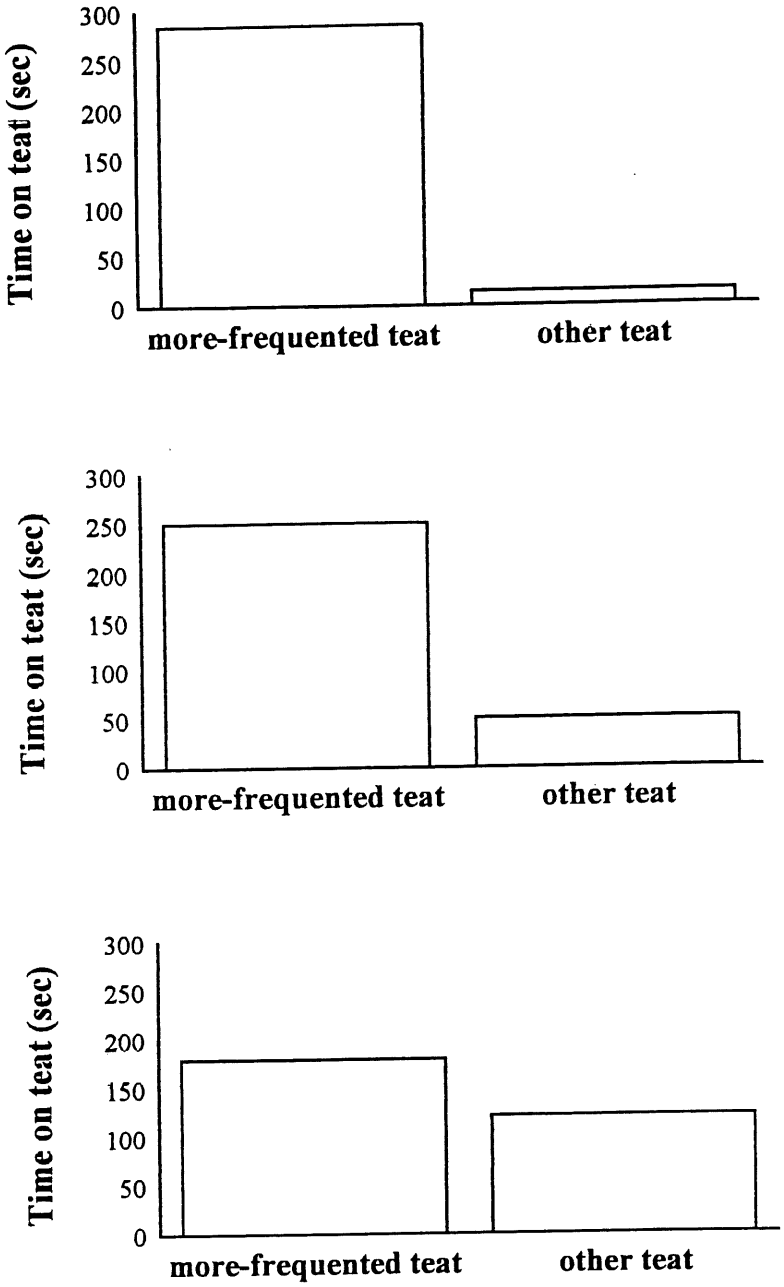

Figure 10. Mean (± standard error) time spent on each teat (Exp. 3) when calves had the choice between 2 nutritive teats where (a) one was at *baseline* and the other at *extremely-slow*; (b) both were at *baseline* and (c) both were at extremely-slow (n = 14).

When both teats were *extremely-slow*, calves switched teats 10 times per minute in the first interval which was more than twice as frequently than in the subsequent intervals (Figure 8b, $F = 101.81$, $P = 0.0001$). Teat-directed behaviour also followed this pattern, occurring 11 times per minute in the first 30 seconds of the meal and only 8 times per minute in the following intervals (Figure 9a, $F = 20.75$, $P = 0.0001$).

When one teat delivered milk at the *extremely-slow* flow rate and the other at the *baseline* flow rate calves behaved similarly to when both teats were at *baseline* (Figures 8 and 9, switching: $S = -0.5$, $P = 1.0$; butting: $S = -13$, $P = 0.14$; stripping: $S = -6$, $P = 0.45$; and releasing: $S = 0.5$, $P = 1.0$). This result may be explained by the fact that calves spent most of their time (95%) on the *baseline* teat (Figure 10a) and therefore, the *baseline* flow rate was the functional flow rate calves were responding to.

3.2 Teat preference

Calves showed a tendency to remain on one teat when both teats were delivering milk at the same rate. When both teats were at the *baseline* flow rate, calves spent 83% of their time on one teat and 17% of their time on the other (Figure 10b). When one teat was at *baseline* and the other was *extremely slow*, calves spent 95% of their time on the *baseline* teat and 5% of their time on the *extremely-slow* teat. At the *extremely-slow* flow rate, calves also spent more time on one teat than on the other (60% vs. 40%, Figure 10c). Across meals, calves did not initiate their meals on one teat any more often than they did on the other ($P > 0.25$).

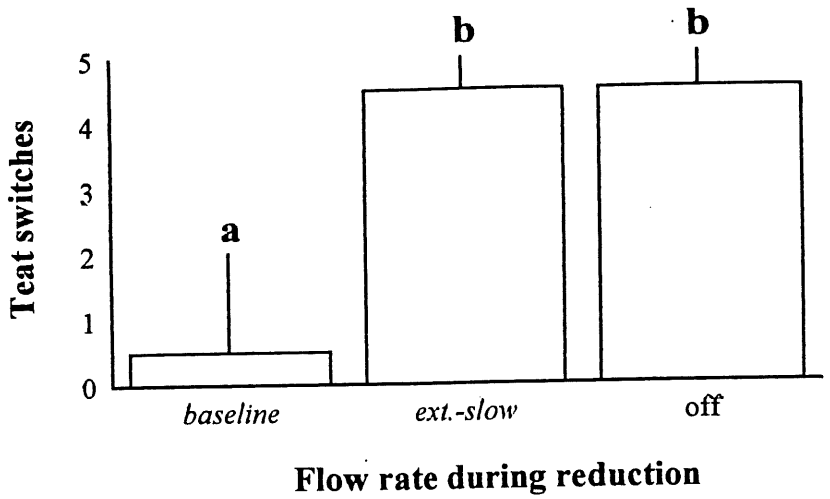

Figure 11a. Teat-switching behaviour following a reduction in flow rate when both teats were nutritive (Exp. 4). Median (and interquartile range) number of repetitions out of 5 in which the calf switched teats following a reduction in milk-flow rate. Medians with different letters differ significantly (n = 14) based on the Wilcoxon paired-sample test.

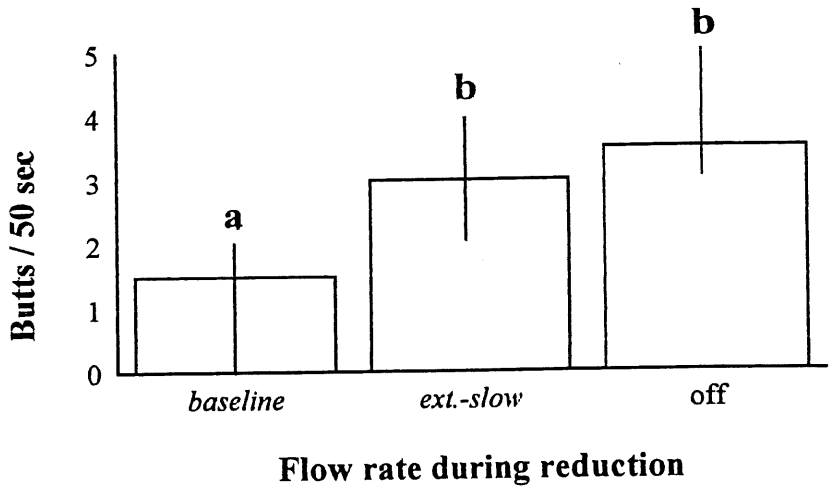

Figure 11b. Butting behaviour following a reduction in flow rate when both teats were nutritive (Exp. 4). Median (and interquartile range) of the total frequency that calves butted over the five 10-second observation periods following milk-flow reduction. Medians with different letters differ significantly (n = 14) based on the Wilcoxon paired-sample test.

3.3 Experiments in which flow rate was suddenly reduced

In experiments 4 to 6, treatment affected switching and butting but had no effect on either stripping or releasing of the teat. When butting was pooled with stripping and releasing, treatment did not have a clear effect on the collective teat-directed behaviours and combining these three variables masked the effect treatment had on butting. In light of this, only the results for switching and butting are presented.

3.3.1 Experiment 4

In this experiment, whether milk flow rate was reduced 16-fold or completely stopped, calves responded similarly. When milk flow rate was reduced from *baseline* to the *extremely-slow* flow rate, calves switched 8 times more often (Figure 11a, S = -52.5, P = 0.0001) and butted twice as frequently (Figure 11b, S = -36.5, P = 0.0024) compared to when flow was maintained at the *baseline* rate (control). The stoppage of milk flow resulted in 9 times more switching (S = -50.5, P = 0.0005) and double the butting (S = -23.5, P = 0.014) seen in the control. There were no differences between the *extremely-slow* treatment and the stoppage treatment in levels of switching (S = -2, P = 0.84) nor butting (S = -0.5, P = 1.0).

3.3.2 Experiment 5

The magnitude of the reduction in milk-flow rate had an effect on switching and butting behaviour. Calves proportionally increased the frequency of these two components of sucking behaviour as the magnitude of the flow reduction increased. When milk flow was reduced by about half (from *baseline* to *slow*), calves performed relatively low levels of switching (Figure 12a) and butting behaviour (Figure 12b), resembling the control treatment in the previous test. When milk-flow rate was decreased by 1/3 (from *baseline* to *very-slow*), calves switched to the

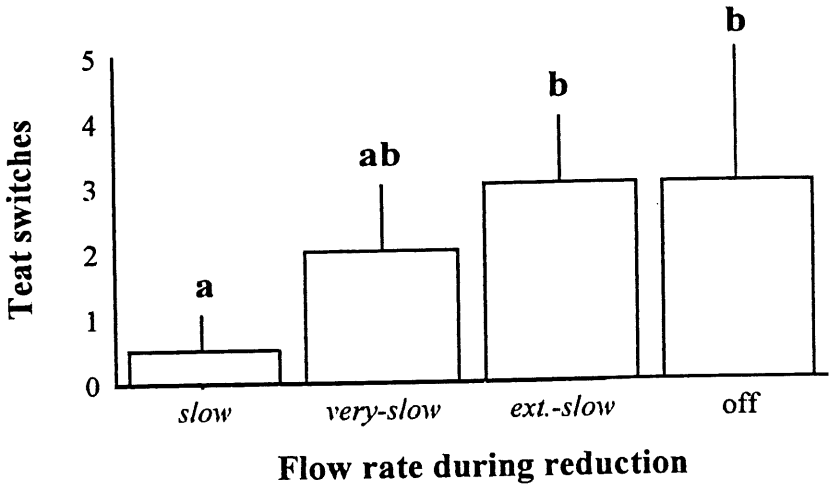

Figure 12a. Teat-switching behaviour following a reduction in flow rate when both teats were nutritive (Exp. 5), looking at the effect of reductions of smaller magnitude (*slow* and *very-slow*). Median (and interquartile range) number of repetitions out of 5 in which the calf switched teats following a reduction in milk-flow rate. Medians with different letters differ significantly (n = 14) based on the Wilcoxon paired-sample test.

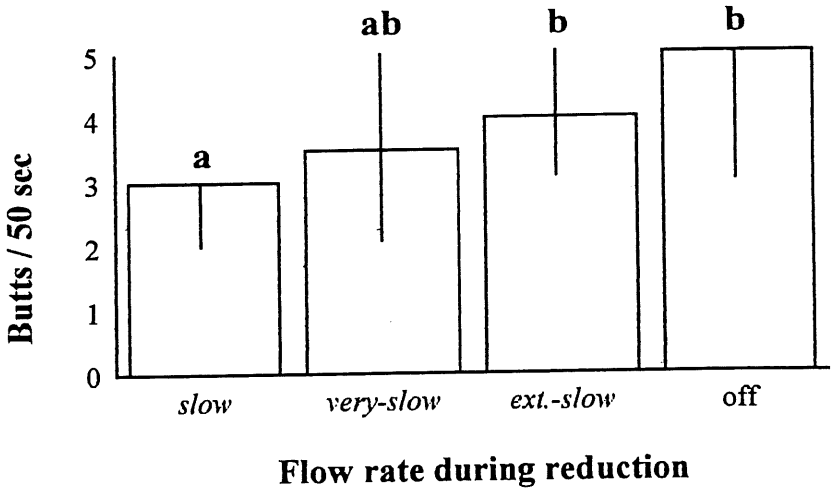

Figure 12b. Butting behaviour following a reduction in flow rate when both teats were nutritive (Exp. 5), looking at the effect reductions of smaller magnitude (*slow* and *very-slow*). Median (and interquartile range) of the total frequency that calves butted over the five 10-second observation periods following milk-flow reduction. Medians with different letters differ significantly (n = 14) based on the Wilcoxon paired-sample test.

other teat a median of 3 times out of 5 and butted a median of 3 times over the five repetitions. These frequencies did not differ from those that resulted from the reduction of flow rate from *baseline* to *slow* (switching: S = 25, P = 0.028; butting: S = 15.5, P = 0.14) nor from *baseline* to *extremely-slow* (switching: S = 14, P = 0.10; butting: S = 19, P = 0.19) nor from *baseline* to off (switching: S = 15.5, P = 0.074, butting: S = 14.5, P = 0.22). When milk-flow rate was reduced 16-fold, from the *baseline* to the *extremely-slow* flow rate or when milk-flow rate was stopped, calves switched teats 8 times more (S = 42.5, P = 0.0015 and S = 42.5, P = 0.0015, respectively) and did slightly more butting (4 instead of 3; S = 36.5, P = 0.0024 and S = 27.5, P = 0.013, respectively) compared to the when flow rate was only reduced from *baseline* to *slow*. There were no differences in behaviour when flow rate was reduced from *baseline* to *extremely-slow* or when flow rate was reduced from *baseline* to off (switching: S = -0.5, P = 0.95; butting: S = -2, P = 0.82).

3.3.3 Experiment 6

Calves responded to a decrease in flow rate when the second teat was dry, similarly as to when the both teats had been nutritive in the previous two experiments. When milk-flow rate was reduced by half (from *baseline* to *slow*), calves switched once out of the five replicates, which was not different from the control (Figure 13a, S = -5, P = 0.51). When milk flow was stopped, calves switched 4 times more frequently than when the flow was reduced to *slow* (S = -34.6, P = 0.0039), and more frequently than when milk-flow rate was not reduced in the control (S = -31.5, P = 0.0029). Butting followed a similar pattern, calves butted more when flow rate was stopped compared to when it was reduced to *slow* (Figure 13b, S = -18.5, P = 0.12) or not reduced at all (S = -29, P = 0.0068). There was no difference between butting rate during the reduction to the *slow* milk-flow rate compared the control (S = -14, P = 0.18).

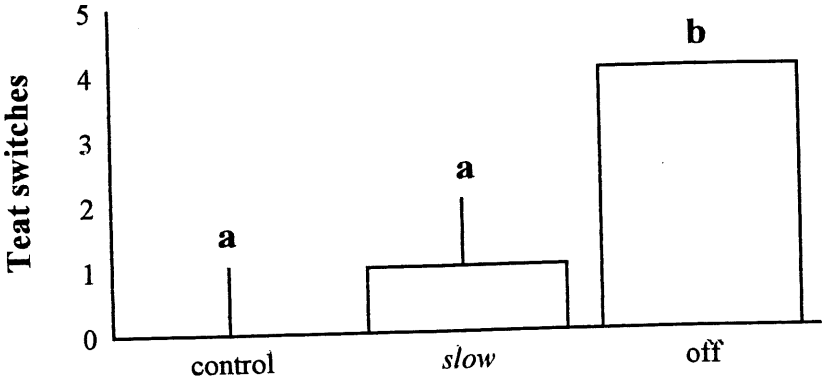

Figure 13a. Teat-switching behaviour following a reduction in flow rate when one teat was nutritive and the other was off (Exp. 6). Median (and interquartile range) number of repetitions out of 5 in which the calf switched teats following a reduction in milk-flow rate. Medians with different letters differ significantly (n = 14) based on the Wilcoxon paired-sample test.

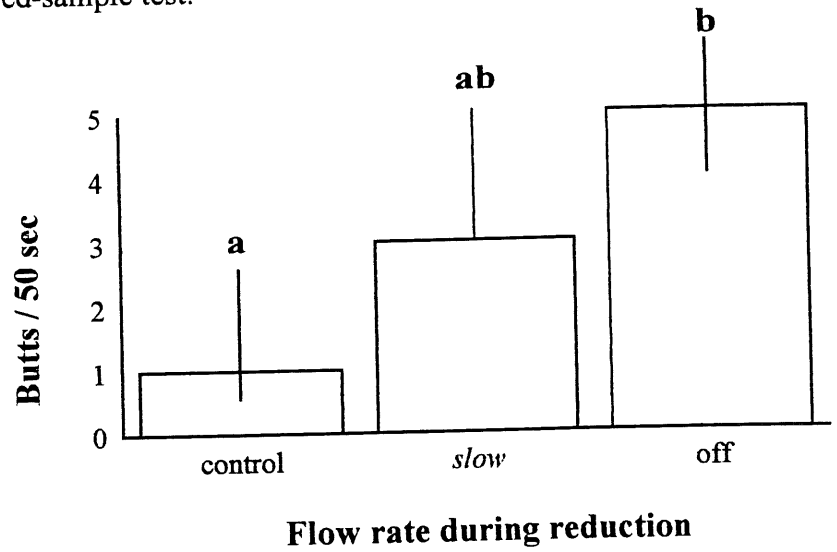

Figure 13b. Butting behaviour following a reduction in flow rate when one teat was nutritive and the other was off (Exp. 6). Median (and interquartile range) of the total frequency that calves butted over the five 10-second observation periods following milk-flow reduction. Medians with different letters differ significantly (n = 14) based on the Wilcoxon paired-sample test.

CHAPTER 4
DISCUSSION AND CONCLUSIONS

4.1 Motivation: the second teat is a stimulus for teat-switching

Calves appear to be highly motivated to switch teats while nursing. The simple presence of a second teat, whether nutritive or dry, acts as a stimulus eliciting relatively high levels of teat-switching behaviour, especially in the first thirty seconds of the meal. This behaviour, which has been termed pre-stimulatory, has been observed previously with calves sucking their dams (Horrel, 1993; Lidfors *et al.*, 1994; Mayntz *et al.*, 1995).

In my experiments, calves sucked milk from a feeding apparatus equipped with two nutritive teats which provided an abundant milk flow as soon as the calf started nursing and this milk-flow rate remained constant throughout the meal. Nevertheless, calves still displayed the initial, characteristic, high-frequency teat-switching followed by a marked decrease after thirty seconds, as seen during a nursing on the dam. In light of this observation, I suggest that the back-and-forth teat-switching behaviour seen at the very beginning of the meal may be an innate, fixed action pattern that is released by the presence of two teats. This behaviour is not dependent on milk-flow rate.

4.2 The initial teat-switching: a fixed action pattern to trigger the milk-ejection reflex

The function of teat-switching at the beginning of the meal may be stimulatory in nature and result in milk ejection. The skin of the teats is highly innervated with pressure-sensitive receptors. When these neurons are stimulated they transmit a message to the hypothalamus which triggers the release of oxytocin into the blood (Schmidt, 1971; Larson, 1985). This hormone is then transported to the udder where it binds to specific receptors that cause the

myoepithelium to contract. This action increases the pressure in the alveoli, squeezing the milk into the udder cisternae at a rapid rate and rendering it available for the calf to drink. It takes approximately 30 to 60 seconds for the milk-ejection reflex to occur (Cross, 1961; Gorewit, 1985; Larson, 1985), which corresponds to the duration of the calf's initial period of high activity at the udder. This coincidence lends support to the idea that in addition to its other functions, such as allowing the calf to receive more milk from another teat, teat-switching behaviour is stimulatory in nature.

The additional benefit derived from switching back and forth between teats, rather than just remaining on one teat, is that a greater number of neurons are stimulated. Stimulating more neurons may be beneficial because sensory stimuli are additive and so milk ejection would be increased compared to the case where only a few neurons were stimulated. In addition, spreading the tactile stimulation from one teat to another would prevent the sensory adaptation that occurs when neural receptors are continuously stimulated (Shepherd, 1988). Therefore teat-switching at the beginning of the meal may be a natural component of nursing that would be adaptive to perform regardless of current milk-flow rate, in order to ensure that milk ejection will occur.

4.3 Milk-flow rate and teat-switching behaviour

My results strongly suggest that flow rate plays a modulatory role in teat-switching behaviour. Teat-switching in the first thirty seconds of the meal was double when both teats were delivering milk at the *extremely-slow* flow rate than when both were at *baseline*, and the rate of switching in the following minutes was also higher, following the same overall pattern as at *baseline*. Calves also responded to either a sudden stop or a sudden decrease to *the extremely-slow* flow rate by switching to the other teat 80% of the time. The probability of switching was proportional to the magnitude of the reduction, demonstrating that when the flow rate was less

drastically reduced from *baseline* the calves were either taking longer to decide whether to switch teats or simply deciding not to.

A non-nutritive second teat did not reduce the calf's motivation to switch teats following a reduction in flow rate as compared to when there were two nutritive teats. Apparently the calves were basing their decision to switch teats on the flow rate of the teat they were sucking and not on their memory of the status of the other teat. It makes sense that calves continued to visit a teat that had been dry throughout the meal because its flow rate may have changed since the calf last checked. This behaviour has adaptive significance since, on the cow, an empty teat would start to refill again. These results demonstrate that calves were very sensitive to changes in milk-flow rate and responded rapidly to a decrease by switching teats.

4.4 Teat switching motivation

Motivation is thought to disappear when a functional goal is attained (Hughes and Duncan 1988; Rushen *et al.*, 1993). Since animals are thought to be motivated to maximise energy intake (Maynard Smith, 1978), it is reasonable to expect that if a calf was not receiving milk at some set rate (the goal), it would be motivated to switch to the other teat. Once it arrived on a teat delivering milk at an acceptable rate, possibly the rate it was used to, the goal would be attained and it would no longer be motivated to switch teats.

My results support this prediction. In Experiment 3, calves switched teats more frequently when both teats were delivering milk at the *extremely-slow* flow rate (0.04 L/min) than when both were at *baseline* (0.66 L/min). Also, in the same experiment, when one teat delivered milk at the *extremely-slow* flow rate and the other at the *baseline* flow rate, the calves spent most of their time (95%) on the faster flowing, *baseline* teat. When they were on the *baseline* teat, they were less likely to switch teats than when they were on the *extremely-slow* teat. Lastly, Experiments 4, 5 and 6 showed that when sucking on a *baseline* teat, calves responded to a reduction in flow rate by switching to the other teat.

Calves still did some teat-switching when both teats were at the *baseline* flow rate. This switching possibly occurred because calves were not satisfied by the *baseline* flow rate or because they were sampling the other teat.

4.5 Teat-switching as a form of environmental sampling

Another function of teat-switching may be to gain knowledge of the milk-flow rate of the different glands of the udder. Animals are known to regularly spend time exploring other feeding sites (Shettleworth *et al.*, 1988) to gather information so they can optimise energy gain in the long run (Maynard Smith, 1978, Krebs and Davies, 1993) by choosing the most profitable sites. The high level of teat-switching observed at the beginning of a nursing in my experiments has also been observed during natural nursings (Horrel, 1993; Lidfors *et al.*, 1994; Mayntz *et al.*, 1995). In my experiments, low levels of teat-switching continued to occur following the initial high-frequency teat-switching at the beginning of the meal at a constant, *baseline* flow rate thus keeping the calf periodically updated on the flow rate of the other teats. Low levels of teat-switching have also been observed during a natural nursing on the dam (Horrel, 1993; Lidfors *et al.*, 1994; Mayntz *et al.*, 1995). Calves demonstrated the usefulness of flow-rate information when they had one *baseline* teat and one *extremely-slow* teat by spending 95% of their time sucking the *baseline* teat.

I observed more frequent teat-switching when both teats were delivering milk at the *extremely-slow* flow rate than when both were at *baseline*. Calves were also more likely to switch teats when the milk-flow rate was greatly reduced compared to when it was only slightly reduced demonstrating that sampling time was inversely proportional to the quality of the feeding site. Animals generally increase their sampling time as the quality of the patch they are exploiting decreases (Kramer and Weary, 1991). When a feeding site is of poor energetic quality and an animal has knowledge that the average feeding site in its environment is of better quality, the potential benefit of finding a better place to feed far outweighs both the cost of searching and the cost of remaining in the poor site (Valone and Giraldeau, 1993), so animals tend to increase their sampling time.

4.6 Butting motivation

In contrast to teat-switching, calves did not butt more frequently during the first thirty seconds of the meal when one or two teats were available. This result differs from two previous reports where butting frequency was indeed higher in the first minute of nursings on the dam (Horrel, 1993; Lidfors *et al.*, 1994). Although the calves in my study were older (18.5 weeks) than the ones in the Horrel study (4-8 weeks), calf age was probably not the reason for the different pattern of butting because data collected from our calves when they were 4.5 weeks old did not reveal an increased frequency of butting in the first minute of the meal (Gaboury and de Passillé, unpublished data). The calves used in the Lidfors *et al.* (1994) study were tracked from birth to 17.5 weeks and higher butting was observed in the first minute of the meal again demonstrating that age was probably not the factor responsible for the different behavioural patterns observed.

Haley *et al.* (1998a) also observed a higher level of butting in the first minute of the meal when calves were feeding from an artificial teat delivering milk at a constant flow rate. Although the feeding systems in my study were very similar to the ones used in the Haley *et al.* study, the diameter of their rubber tubing was four times greater than in my study (1.6 vs. 0.4 cm), possibly resulting in calves' having to apply increased suction to maintain milk flow from the teat. This difference may have been responsible for the different levels of butting observed in each experiment.

Although other studies suggested that there is a high incidence of butting at the beginning of the meal, the absolute frequencies and the magnitude of the decreases were quite different. On the dam, Lidfors *et al.* (1994) reported 0.6 butts in the first minute, 0.2-0.4 butts in the next minute (a 2- to 3-fold decrease) and then an increase over the next 3 minutes. Horrel (1993) reported 3 butts in the first minute, declining to 0.3 in the next minute (a 10-fold decrease) and then increasing in the following 3 minutes. The absolute differences in butting frequency

between the Horrel study and the Lidfors *et al.* study might have been due to different definitions of butting.

In my study, when calves had one *baseline* teat to suck from, calves butted about 1.2 butts/min. However, when they had two *baseline* teats available, butting rate doubled (2.5 butts/minute at *baseline*, 0.66 l/min). At mealtime, it appeared that having two teats which would potentially deliver milk increased calves' overall arousal and that the additional energy got translated into increased butting behaviour. Results from my study might have differed from those of Horrel and the Lidfors *et al.* studies because they observed calves that were nursing the dam. Since flow rate from an udder may not be constant and/or may decrease as time elapses, changes in flow rate would have affected butting (Haley *et al.*, 1998a).

As with teat-switching, the rate of butting was dependent on the flow rate from the teat the calf was sucking and not the flow rate from the second teat. At the *baseline* flow rate, levels of butting were similar regardless of whether the calf had one nutritive teat, a combination of one nutritive teat and one dry teat, or two nutritive teats. There was an overall increase in butting when the calves had two nutritive teats at the *extremely-slow* flow rate and also when there was a sudden decrease in milk-flow rate. As with teat-switching, the greater the decrease in milk-flow rate, the higher the frequency of butting. This may be because butting acts to stimulate the milk-ejection reflex and may possibly be a mechanical stimulus for milk ejection (Cross, 1954; Findlay and Grosvenor, 1967). Based on my results, butting is not a fixed action pattern that occurs at the beginning of the meal, independently of a reduced milk flow.

4.7 Other behaviours

I examined teat-releasing and teat-stripping behaviour and found that their frequencies were quite variable and their distributions were not normal. When the frequencies of these two behaviours were added to that of butting, the patterning throughout the meal resembled that of teat-switching: a higher frequency in the first thirty seconds of the meal, compared to the

intervals that followed. This pattern was only observed when there were two teats, but it occurred at *baseline* and at the *extremely-slow* flow rate. In the experiments in which milk-flow rate was suddenly reduced, unlike teat-switching and butting, there were no differences in teat-directed behaviours among treatments.

It is not clear whether releasing the teat and teat-stripping are distinct behaviours or if they are components of switching and butting. Stripping was quite variable ranging from a simple sliding of the mouth on the teat to an aggressive, downward slide, followed by a release but without the ensuing upward movement of the butt. Similarly, a teat-release may simply have been an incomplete switch, or a less energetic strip. I therefore conclude that these behaviours either individually or grouped as "teat-directed behaviours", were not reliable indicators of a reduced milk-flow rate.

4.8 Teat preference

Calves on the dam often have a teat preference (Horrel, 1993; Mayntz, 1996), usually for the front teats (Hafez and Lineweaver, 1968; Selman *et al.*, 1970; Edwards and Broom, 1982; Lidfors, 1994) possibly due to a higher milk production in the anterior glands (Hurley, 1998) or to stay clear of the mother's hind limbs and thus avoid kicks. In my experiments, when each teat delivered milk at a different rate (one at *baseline* and one at *extremely-slow*), calves spent 95% of their time on the *baseline* teat and only 5% of their time on the *extremely-slow* teat. This result is consistent with the observation that calves on the dam preferentially nursed from the higher producing teats. Teat location was randomised to eliminate any effect it might have had on preference.

When both teats had the same flow rates (either both were at *baseline* or both were at *extremely-slow*), calves did not show a consistent preference for one teat over another, across meals. However, within a meal, calves did spend more time on one teat than the other. This may be due to positive feedback whereby animals tend to persist in an activity they have

already begun (Wiepkema, 1971; Toates, 1986; Jensen and Toates, 1993). Calves showed less preference for a given teat, within a meal, when both teats were *extremely-slow* than when both were at *baseline*. This was most likely caused by an insatisfaction with the *extremely-slow* flow rate they were experiencing which stimulated them to switch teats more and thus not remain on the same teat for as long.

4.9 Conclusions and implications

It is not known how milk-flow rate normally changes during a natural nursing. It is generally assumed to be slow at the beginning, before the occurrence of the milk-ejection reflex, and then slow again at the end of a sucking episode on a teat, when the calf has drained that quarter of the udder (Lidfors *et al.*, 1994; Mayntz *et al.*, 1996). This deduction was prompted by the observation that calves teat-switched and butted at high frequencies during these periods. Flow rate from the udder during a nursing has not been measured so by identifying how flow rate motivates the behaviours seen during these periods, flow rate of the udder can be inferred by observing behaviour.

The motivation for teat-switching at the beginning of the meal appears to be endogenous. Calves teat-switched and performed teat-directed behaviours (butt + release + strip) at high frequencies during the first thirty seconds of meals and then the frequencies of these behaviours decreased drastically but did not disappear, despite a constant flow rate, when two teats were available. Butting did not follow a similar pattern, remaining constant throughout the first 2.5 minutes of the meal. A reduced flow rate motivated calves to switch teats and to butt and this was true if the reduction was sudden or constant over time. The teat-switching and butting responses were proportional to the magnitude of the reductions. The effect of a sudden reduction in flow rate on teat-releasing and teat-stripping remains unclear. Calves based their behavioural decisions on the flow rate of the teat they were exploiting, so that the state of flow in the other teat did not affect these decisions. However, calves may have been

continuously monitoring the flow rate in the other teat in order to have an overall evaluation of their environment.

Although it is impossible to determine whether the function of teat-switching behaviour is for the calf to stimulate the mother's udder or to sample its environment, I suggest that it is quite conceivable that teat-switching has both these functions as they would both lead to maximising milk intake. Sucking and the various behaviours involved in a nursing are so important for the health, survival and reproduction of the calf that if a given behaviour aids in optimising the milk removal process in various ways it would have been even more highly selected for than if it only had one function (Lefcourt and Akers, 1966).

The results of this study suggest that teat-switching and butting are useful behaviours for inferring possible flow-rate problems in calves on the dam or calves nursing from an artificial teat. It is important however, not to interpret the initial, frenetic teat-switching as resulting from a reduced milk-flow rate. Instead, this seemingly sub-optimal behaviour is likely used by the calf to stimulate milk flow from the cow and to gain knowledge of the flow rate of different teats and would therefore be selected for and maintained in the species. These results could also be applicable to other ungulates as an indicator of milk-flow rate during a nursing, given their phylogenetic relationship to domestic cattle.

APPENDIX A

Quantities of milk fed to calves

Period beginning (1996)	Average age of calves (weeks)	Milk Replacer (120 g/l) fed (l/period)	Hay given (g/period)
April 15[1,2,3]	1.5	20.0	400
April 22[4]	2.5	25.0	700
April 29[5]	3.5	22.7 (L) / 23.0 (H)	500
May 4	4	44.0 (L) / 46.4 (H)	700
May 11	5	52.9 (L) / 57.0 (H)	800
May 18	6	58.8 (L) / 68.8 (H)	1 400
May 25	7	73.1 (L) / 80.0 (H)	1 400
June 1	8	84.5 (L) / 91.5 (H)	1 400
June 8	9	94.8 (L) / 101.8 (H)	1 400
June 15	10	95.6 (L) / 102.3 (H)	1 700
June 21	11	94.4 (L) / 98.4 (H)	1 400
June 29	12	147.8 (L) /258.3 (H)	6 300
July 20	15	86.1	2 800
July 27	16	93.1	2 800
August 3	17	93.1	2 800
August 10	18	93.1	2 800
August 17	19	93.1	2 800
August 24	20	93.1	2 800
August 31	21	93.1	2 800

1) April 15: Calves arrived from being bought, the received no milk.
2) Calves received 2 l/day of electrolyte solution (last day: April 25).
3) Hay was given starting on April 18.
4) Water was given *ad libitum* starting on April 26.
5) Due to the problem of calves not finishing their meals, 2 groups were created: the first composed of the heavier calves (H) and the second composed of the lighter ones (L). From April 29 – July 19, the calves in the lighter group were given slightly lower quantities of milk replacer than the ones in the heavy group.

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